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Reducing uncertainty in predictions of the response of Amazonian forests to climate change.

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Declaration

I confirm that this work is my own, except where indicated otherwise. No part of this thesis has been submitted for any other degree or qualification.

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A close approximation to my view of science:

"Nothing would be what it is because everything would be what it isn't.

And contrary-wise; what it is it wouldn't be, and what it wouldn't be, it would.

You see?"

From Alice's Adventures in Wonderland, by Lewis Carroll (1865).

Abstract

Amazonia contains the largest expanse of tropical forest in the world and is globally significant as a store of carbon, a regulator of climate and an area of high species diversity. The ability of the Amazonian forests to maintain these important ecological functions is however, increasingly under question in light of recent predictions of climate change. There is currently significant uncertainty in model predictions of how Amazonian forests will respond to predicted future climate change. This thesis reports the finding of two field studies, targeted at understanding the responses of two tropical forest carbon fluxes which are poorly simulated in vegetation models, and two modelling studies, which aim to better quantify uncertainty on model predictions of the effects of current and future climate change on the ecological function of Amazonian forests.

The responses of forests to varying magnitudes of seasonal changes in climate which occur across Amazonia can give an important insight into the sensitivity of these forests to climate perturbations and changes. Testing the sensitivity of an Amazonian forest in Tambopata, Peru, to seasonal variations in precipitation and temperature, I find that the stem diameter growth of tropical trees is more sensitive to water availability than temperature changes. The vulnerability of trees to reduced soil water varied between tree classes with different functional traits, including wood density, tree height, tree diameter and tree growth rate. Similarly, I find that the respiration flux from tropical dead wood, at a second site in French Guiana, is highly sensitive to variations in water content. I show that these variations in respiration fluxes can be modelled successfully using seasonal variations in soil water content.

To date there are few studies which have comprehensively tested vegetation models using ecological data from Amazon forests. Using data assimilation and nine sources of ecological data I estimate the certainty with which we can parameterise a carbon cycle model to represent the effects of a strong dry season on tropical forests. Using this technique I find, that the carbon balance of Amazonian forests can be very sensitive to reductions in water availability, and that these seasonal changes need to be accurately simulated across models to correctly predict annual carbon budgets.

The variability in model responses caused by differences in the way processes are structured and parameterised in vegetation models requires better quantification. Using a model inter-comparison I demonstrate that the relative sensitivity of modelled climate-vegetation feedbacks to changes in ambient air temperature and precipitation is highly variable. I find that although the models showed similar directional responses at both the leaf and canopy scale some models showed a greater sensitivity to temperature and others to drought. I therefore demonstrate the need for greater constraint on modelled responses of Amazonian forests to changes in temperature and precipitation.

The impact of climate change on Amazonian forests is an important global issue, yet our knowledge is reliant on our ability to understand the uncertainties on our predictions. Using field data to evaluate and to develop model predictions is a valuable way to reduce the uncertainty associated with modelling future change. This thesis presents an investigation of how tropical forests respond to changes in climate and with what certainty we can model these changes in order to predict the response of Amazon forests to predicted future climate change.

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Chapter 1: Introduction

1.1 Overview

Tropical forests have the highest levels of gross primary production in the world (Beer et al., 2010). The Amazon region contains the largest expanse of humid tropical forest, covering an area of 6.3x 10^6 km^2 (Eva et al., 2004) and it plays an essential role in regulating regional and global climate. Amazonian forests are predicted to store between 69 and 102 Pg of carbon in biomass (Saatchi et al., 2007). They are an important carbon sink, sequestering an estimated 0.39± 0.26 Pg C yr^{-1} (Gloor et al., 2012), and thus reducing the rate at which the atmospheric concentration of carbon dioxide (CO_2) is increasing. The combined effects of climate and land use change are, however, bringing the state of the Amazon as a carbon sink into question (Davidson et al., 2012). Gloor et al. (2012) estimated that during the period following a major drought event in 2005 (2005–2009) the Amazon forest became a 0.66±0.23 Pg C yr^{-1} source of carbon to the atmosphere. The importance of Amazonian forests as a carbon store, source of biodiversity and a regulator of climate make understanding the sensitivity of its carbon balance to changes in climate a priority for scientific research.

Recent severe drought events in the Amazon (Marengo et al., 2008; Marengo et al., 2011) significantly increased tree mortality rates (Phillips et al., 2009; Phillips et al., 2010). Although substantial uncertainty exists among climate model predictions for

the 21st century, such events could become more common in Amazonia as atmospheric CO_2 levels rise (Cox et al., 2008), as could the development of longer, more intense dry seasons (Christensen et al, 2007; Malhi et al., 2009a; Jupp et al., 2010; Marengo et al., 2012). To understand the implications of such possible changes, the sensitivity of these forests to changes in climate, particularly changes in temperature and soil water availability, need to be resolved with greater certainty.

The necessity to understand the consequences of climate change has made modelling an increasingly important tool in researching the biophysical functioning of Amazonia. In order to use models effectively as part of our efforts to understand the biophysical functioning of Amazonia, they must be tested rigorously. Targeting data collection towards process-level responses by components of a forest ecosystem, and towards responses which are poorly understood, is an efficient way to develop greater model constraint. Analyses which employ data-model integration and inter-model comparison are also valuable tools for understanding and reducing the uncertainties associated with making predictions of the responses of tropical forests to climate changes. This chapter will briefly review the current processes and uncertainties involved with predicting the effects of climate change on the carbon stock and ecological function of Amazonian forests, and the value of investigating and testing models against seasonal data. A brief overview is also given of the structure of this thesis, and chapters therein.

1.2 Current predictions of the effects of climate change on Amazonian forests

The first study to predict large-scale losses of Amazonian forest in response to 21st century climate change was White et al (1999), who used the Hybrid vegetation model, forced with climate data from the HadCM3 global circulation model (GCM). Following this study Cox et al. (2000) re-enforced this result, publishing the first Earth System model study to fully couple a GCM (HADCM3) with a dynamic vegetation model (TRIFFID). This and several subsequent studies have found a large modelled reduction in rainfall across the Amazon region, resulting in significant losses of Amazonian forest cover. This modelled outcome has been termed 'Amazon die-back' (Cox et al., 2000; Betts et al., 2004; Cox et al., 2004).

Since the concept of 'Amazon die-back' was created following the results of the studies described above, there has been significant debate surrounding these results. Assessing such vulnerability to drought requires an understanding of the climate risk, the response by vegetation to climate and the climate-vegetation feedback. There exists substantive inter-model variability in how GCMs simulate fine-scale and regional patterns of future rainfall (Malhi et al., 2009a; Jupp et al., 2010). Regional rainfall patterns strongly affect forest water constraints and therefore variations in future predictions of regional rainfall cause variability in future predictions of biomass change across Amazonia (Rammig et al., 2010). A study by Salazar et al. (2007) showed that large-scale loss of Amazon vegetation was much more common using the climate data from the HadCM3 GCM, which simulates a drier climate than other GCMs. However, the climate data from HADCM3 is still commonly used to

drive vegetation models which make predictions on climate change in Amazonia (Harris et al., 2008; Huntingford et al., 2008), possibly because it provides accurate representation of other atmospheric processes, such as El Niño- Southern oscillation (Cox et al., 2000).

Reductions in rainfall are likely across Amazonia, although the drought impact of such reductions on Amazonian forests remains uncertain and dependent on regional variability in climate responses (Jupp et al., 2010; Marengo et al., 2012) and the effect of the interaction of land use change, with climate forcing and vegetation change (Meir and Woodward, 2010). Although there is a risk of substantial drought in Amazonia, especially in the north east region (Harris et al., 2008; Huntingford et al., 2008; Sitch et al., 2008; Galbraith et al., 2010; Jupp et al., 2010), the predicted ranges of changes in climate by 2100 remain large for both temperature (1.8–8°C) and rainfall (-21% – +6%) (Christensen et al, 2007; Malhi et al., 2009a; Marengo et al., 2012). In addition to future alterations in climate the complexity of the feedback with vegetation means that current understanding of how sensitive the carbon balance of these forests is to changes in temperature and precipitation remains uncertain (Friedlingstein et al., 2006; Sitch et al., 2008; Galbraith et al., 2010; Poulter et al., 2010). Model predictions of substantial responses to climatic drought in Amazonia may actually be derived from high model sensitivity to changes in temperature rather than precipitation (Galbraith et al., 2010). Ground data has however shown that Amazonian forests are very sensitive to drought (da Costa et al., 2010; Phillips et al., 2010; Kumagai and Porporato, 2012), hence there is a need to develop a better understanding of the vegetation feedbacks and their uncertainties within land surface models.

1.3 Difference in model structure and its influence on simulating the response of Amazonian forests to climate change

Predicting future climate change in Amazonian forests is a process which involves multiple stages, described in Figure 1.1. Stages 2 and 3 in Figure 1.1 require the use of global circulation models (GCMs), which are coupled to vegetation models, which simulate the responses of the vegetation to climate in stages 4 and 5. Each dashed box shown in Figure 1.1 can be interpreted as a source of uncertainty in each of the stages of making future predictions. Figure 1.1 demonstrates that modeling climate change is not a simple linear process, but involves multiple and continuous feedbacks between different stages of prediction. Quantifying the effects of these feedbacks is difficult and these feedbacks serve to amplify uncertainty over time; quantifying this uncertainty and the effect of these feedbacks is therefore complex (Friedlingstein et al., 2006). Uncertainty on climate change prediction can be split into three components: model uncertainty, uncertainty from internal variation in the climate system, and uncertainty from climate scenarios (Hawkins and Sutton, 2009). Model uncertainty has been found to be the largest component of total uncertainty until the model prediction time goes beyond 50 years (Hawkins and Sutton, 2009; Meehl et al., 2009). Reducing the uncertainty associated with model structure and parameterisation is therefore an important way to reduce the uncertainty on future climate change predictions.

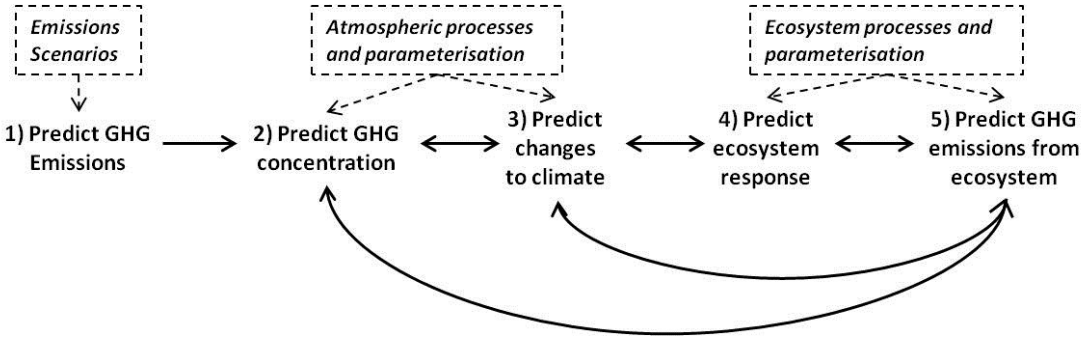

Figure 1.1: Schematic diagram of the processes and uncertainties involved in modelling future climate change. Modelling uncertainties are shown in dashed boxes.

Different model structures represent different interpretations and solutions for incorporating these complex processes into a logical structure, which represents the ecological function of an ecosystem. Models can vary in type, for example: dynamic global vegetation models (DGVMs) which are designed to be used globally and thus simulate different plant functional types (e.g. JULES; Clark et al., 2011, CLM; Baker et al., 2008); gap models which simulate the structure of individual trees and forest succession (e.g. ED; Medvigy et al., 2009); process-based vegetation models, which simulate ecological function in greater detail (e.g. SPA; Williams, 1996); and models which simulate a single ecological component, for example soil models (e.g. RothC). As well as these variations in model type, within models of each type there are also differences in vegetation structure and model parameterisation, which are likely to simulate different sensitivities to changes in climate.

Variation in both the structure and parameterisation of models has been shown to introduce significant variance among future predictions of carbon-climate cycle

feedbacks (Friedlingstein et al., 2006; Meir et al., 2006; Huntingford et al., 2008; Galbraith et al., 2010; Poulter et al., 2010). A study using five dynamic global vegetation models demonstrated that for an extreme climate change scenario (A1F1) the cumulative uptake of carbon varied by 494 Pg C (11-505 Pg C), between the five models in the 21st century (Sitch et al., 2008). Reducing high inter-model variability requires a greater understanding of how process representation varies between different model structures, how this interacts with the sensitivity of particular models to variations in climate, and how well this variation relates to reality. Inter-model comparisons are now becoming an increasingly common way to address such issues (Friedlingstein et al., 2006; Huntingford et al., 2008; Luo et al., 2008; Sitch et al., 2008; Galbraith et al., 2010), though there remains a limitation on data availability for model testing; this is where the information provided by model inter-comparisons can be examined and used for model development (Jupp et al., 2010; Rammig et al., 2010).

Model inter-comparisons, although valuable for determining the uncertainties associated with variations in model structure, do not provide information on the uncertainty associated with how individual models are parameterised. In fact, model uncertainty introduced to the carbon-cycle feedback from parameter selection is currently not accounted for in current climate change predictions. A recent modelling sensitivity analysis has however shown, that using a single climate change scenario the uncertainties introduced by varying six vegetation parameters creates larger uncertainty than that associated with the IPCC SRES scenarios (Booth et al., 2012). Quantifying how parameter uncertainty influences model output, is therefore important to provide accurate estimates of uncertainty on predictions of future

change over Amazonia.

Reducing uncertainty in model projections requires testing models against data and identifying sources of uncertainty in model parameterisation and model structures; however this is only possible using historical data. Identifying the uncertainties of simulating the current climate, particularly the strong seasonal variations which occur in some Amazonian forests, can provide a valuable insight into the existing uncertainty in model projections for climate change in the Amazon. As Amazonian forests have, in multiple studies, been shown to be relatively close to carbon neutral (Chambers et al., 2004; Hutyra et al., 2007; Bonal et al., 2008; Malhi et al., 2009b) small changes in either respiration or gross primary productivity (GPP) could substantially alter the carbon balance. Currently however, the influence of seasonal climate on these processes remains poorly quantified. The uncertainty associated with predicting respiration is probably greater than uncertainties associated with predicting how climate change impacts GPP in tropical forests, reflecting in part an historical bias towards estimating GPP (Meir et al., 2008). To account for this I will first discuss the uncertainties associated with seasonal variations in gross primary production (GPP) in tropical forests and the implications for modelling (Section 1.4), and then move on to discuss those associated with seasonal variation in respiration and the implications for modelling (section 1.5).

1.4 Uncertainties associated with simulating seasonal patterns of GPP in tropical forests

Despite the complexity of tropical forests, recent developments in vegetation models have demonstrated that models can simulate seasonal changes in forest productivity (Saleska et al., 2003; Fisher et al., 2007; Baker et al., 2008). Simulating deep rooting systems in models, which have been shown to provide access to deep water during the dry season (Nepstad et al., 1994; da Rocha et al., 2004; Oliveira et al., 2005) has improved model simulation of seasonal changes in GPP (Saleska et al., 2003; Lee et al., 2005; Baker et al., 2008; Grant et al., 2009). Such work suggests that these forests may be more resilient to reductions in water availability than earlier predictions suggested (Tian et al., 2000; Botta et al., 2002). However, it should be noted that a recent study has demonstrated that deep water uptake by roots may be relatively limited and cease to occur over periods of prolonged drought in the Amazon (Markewitz et al., 2010). Therefore care must be taken when applying observed climate responses on a seasonal timescale to longer time periods.

The progression from wet to dry season has also been a focus. Studies in Amazonian forests have shown that the transition from wet to dry season can both increase (Saleska et al., 2003; da Rocha et al., 2004; Goulden et al., 2004; Hutyra et al., 2007; Bonal et al., 2008) and decrease (Malhi et al., 1998; Chambers et al., 2004; Keller et al., 2004) the net ecosystem productivity (NEP). The reasons for such variability in responses from different Amazonian forests are likely a function of both edaphic variation and differences in vegetation properties.

Some remote-sensing studies have suggested that there is a 'greening-up' of Amazonian forests in the dry season (Huete et al., 2006; Myneni et al., 2007; Saleska et al., 2007). The suggestion has been that Amazonian forests flush new, more physiologically efficient leaves during or just before peak dry season, which increases GPP. However, the results from these remote-sensing studies remain debated: one line of argument suggests that the remote sensing data has been misinterpreted and that variations in leaf optical properties rather than leaf area cause the perceived 'green-up' (Samanta et al., 2010; Samanta et al., 2012); another suggests the mechanism for the 'green-up' is misinterpreted by not accounting for increased mortality in the dry season, which alters the forests structural and reflective properties (Anderson et al., 2010); a third argument suggests that current remote sensing data are not of sufficient quality to resolve such changes in these forests (Asner and Alencar, 2010). Seasonal patterns in phenology and associated changes in photosynthetic efficiency (Wright et al., 2004) are important controls on seasonal changes in GPP. Seasonal changes in GPP are not, however synchronous with seasonal changes in tropical forests' tree growth. Data from dendrometer studies from forest sites across the tropics have suggested that tropical tree growth is lower in the dry season, when soil moisture content is reduced (Clark et al., 2010; da Costa et al., 2010; Chaturvedi et al., 2011; Wagner et al., 2012; Malhi et al., 2013; Rowland et al., in review). Temperature may however, also be important; studies of tree growth from a forest in La Selva, Costa Rica, Central America and Pasoh, Malaysia, SE Asia suggested that tropical trees are most limited in years when annual temperatures are higher (Clark et al., 2003; Feeley et al., 2007). Understanding how climate limits tree growth is important and likely benefits from an understanding of

carbon allocation patterns. Correctly simulating carbon allocation is important for predicting the effects of changes in GPP on tropical forest function. Changes in the patterns of carbon allocation to leaves, roots and stems, between wet and dry season have been observed in forests across the Amazon (Aragão et al., 2009; Malhi et al., 2011; Malhi et al., 2013). However, the timing and causes of changes in allocation patterns in tropical forests still remain poorly resolved.

Simulating the phenology of Amazonian forests in models also remains a challenge (Verbeeck et al., 2011). Periods of leaf peak annual litter-fall, and presumably new leaf growth are common in Amazonian forests, just before or during the dry season (Chave et al., 2010). The flushing of new leaves is associated with increases in photosynthetic efficiency (Wright et al., 2004); therefore leaf flushing is likely to increase photosynthesis. However, the timing of maximum leaf loss is variable across Amazonian forests (Chave et al., 2010) and the causes of leaf flush remain poorly understood (O'Brien et al., 2008). Poor understanding of this process has made it difficult to parameterise models (Verbeeck et al., 2011) and the effects of changes in phenology with climate and the impact of this on productivity remains uncertain.

1.5 Uncertainties associated with simulating seasonal patterns of respiration in tropical forests

Understanding changes to the amount of carbon lost through ecosystem respiration (R_{eco}) is as important to understanding NEP as alternations in GPP, but there has

been much less focus on R_{eco} (Meir et al., 2008). R_{eco} comprises five major components: leaf, live wood and root respiration (autotrophic components) and, soil and dead wood respiration (heterotrophic components). Effectively quantifying R_{eco} requires understanding each process separately, as they respond to climate in different, semi-independent ways.

Recent studies from tropical rainforests have demonstrated that natural variation in moisture availability rather than temperature imposes a greater control on seasonal and inter-annual changes in heterotrophic respiration; depending on the initial moisture status of the soil, drought related decreases in soil moisture can cause both decreases (Chambers et al., 2004; Sotta et al., 2004; Metcalfe et al., 2007; Sotta et al., 2007; Bonal et al., 2008; Kosugi et al., 2008; Ohashi et al., 2008; Wood and Silver, 2012) and increases (Schwendenmann et al., 2003; Cleveland et al., 2010) in soil CO_2 flux. Despite this, many dynamic global vegetation models simulate stronger temperature than moisture responses for heterotrophic respiration in the tropics (Sotta et al., 2007; Baker et al., 2008; Galbraith et al., 2010). Few models account adequately for the observed reductions in heterotrophic respiration with reductions in dry season soil water availability in the tropics (Sotta et al., 2004; Sotta et al., 2007; Bonal et al., 2008; Meir et al., 2008; Rowland et al., in reveiw). However, an experimental modelling study has demonstrated that altering the sensitivity of soil respiration to changes in soil moisture can significantly improve the simulation of the seasonal carbon budget of tropical forests (Baker et al., 2008).

Some sources of heterotrophic respiration are not simulated at all in current models. For example, respiration from coarse woody debris (R_{cwd}) is, in most but not all

models, incorporated into the estimated soil respiration flux. This mostly reflects the limited empirical basis for estimating the size of this flux and its response to changes in climate (Chambers et al., 2001). Alterations to R_{cwd} may however, have important consequences when unpicking seasonal changes in the carbon balance, particularly in situations where past or future tree mortality rates have been, or are predicted to be, high (Huytra et al., 2007).

The autotrophic components of R_{eco} derive from leaves, wood and roots. The responses of autotrophic respiration to variability in available soil water and seasonal variations in climate are more variable than that of heterotrophic respiration. Currently reductions in available soil water have been found to cause a ~30% reduction to average stem respiration at a site in French Guiana (Stahl et al., 2011), but no significant reduction at a drought experiment site in north east Brazil (Metcalfe et al., 2010b); similarly no seasonal change was observed in Costa Rican forests (Cavaleri et al., 2006), however these forests are almost a-seasonal relative to the two previous examples. In contrast, long term reductions in water availability have been found to increase fine root respiration on a drought experiment in the eastern Amazon (Metcalfe et al., 2010b). Despite expecting leaf respiration to decrease as photosynthesis decreases (Atkin and Macherel, 2009), Stahl et al. (in press) show no significant change in leaf respiration to match seasonal changes in GPP (Bonal et al., 2008); and after four years of drought a ~23% increase in leaf dark respiration was found in eastern Amazonia, contrasting overall reductions in GPP (Metcalfe et al., 2010a; Metcalfe et al., 2010b), although the exact effects of long term drought on leaf respiration remain unclear (Atkin and Macherel, 2009).

The variability in the observed responses of autotrophic respiration to changes available moisture may reflect complexity in the contributory processes themselves. For example, Atkin and Macherel (2009) demonstrate that there are multiple possible responses of different leaf respiratory pathways to water stress, which, when combined could produce either higher or lower respiration rates in response to water stress. The variability in observed responses may also reflect complexity associated with interpreting or scaling respiration measurements; for example partitioning growth and maintenance respiration (Mccree, 1974; Ryan et al., 1994; Damesin et al., 2002; Meir and Grace, 2002), determining the origin of measured respiration fluxes, especially from woody stems (Levy et al., 1999; Teskey and McGuire, 2007), and determining whether fluxes should be scaled on a mass or surface area basis (Levy and Jarvis, 1998; Meir and Grace, 2002; Cavaleri et al., 2006).

The complexity associated with the response of autotrophic respiration to changes in water availability and other climatic variables, means that without further insight, attempting to simulate such detailed responses in vegetation models is currently more likely to be counterproductive for improving model accuracy. Consequently, at present, vegetation models tend to have a highly simplified simulation of autotrophic respiration. In most models autotrophic respiration is generally considered to be a fixed fraction of GPP (Waring et al., 1998; Williams et al., 2005) or is a product of GPP and a simple, normally exponential, temperature response function. Previously the adequacy of such simple models of autotrophic respiration has not been adequately tested in tropical forests, primarily because of a paucity of data from all components of autotrophic respiration to allow a comprehensive assessment. Currently, however there are increasing numbers of forests plots at which time series

data from multiple autotrophic components is now becoming available and this provides an excellent mechanism by which to test and improve how autotrophic respiration is simulated in models.

Understanding seasonal changes in tropical forests can give an important insight into the function of not just Amazonian but right across tropical forests. Across the tropics increased mortality most commonly occurs from short intense seasonal drought events rather than multi-year drying (Allen et al., 2010). Consequently understanding the effects of seasonal changes in climate on tropical forest function can provide important insights for interpreting the impacts of future climate change. This may be particularly important for Asian tropical forests, which are more sensitive to drought than Amazonian forests (Phillips et al., 2010) and predicted to suffer significantly increased mortality with predicted increase in the frequency and intensity of dry periods (Kumagai and Porporato, 2012). Interestingly eddy covariance data has demonstrated that despite some Malaysian forests being close to a-seasonal they still demonstrate reduction in ecosystem respiration in response to small seasonal reductions in soil moisture (Kosugi et al., 2008), suggesting that small variations in seasonality may still be important in relatively a-seasonal climates.

A greater understanding of the sensitivity of the processes involved in productivity and respiration from Amazonian forests can provide a basis through which model structure and parameterisation can be improved. In the next section I will describe how I address three key areas of uncertainty discussed in the previous sections (uncertainty associated with ecological processes, model parameter uncertainty and model structure uncertainty) with the overarching aim of improving our ability to

simulate the response of tropical forests to changes in climate.

1.6 Overview of Thesis

1.6.1 Aim

The aim of this thesis is to contribute to reducing the uncertainty associated with how sensitive Amazonian rainforests are to changes in climate. To address this aim I use a combination of empirical and modelling studies. Data are used from three sites across Amazonia: one site in Tambopata, south-east Peru, experiences a seasonal climate which is close to the average seasonality across the Amazon basin; a second site on the east coast of French Guiana was selected because of the existence of strong seasonal drought which occurs at the site in response to the movements of the inter-tropical convergence zone; and a third site used in this study is a through-fall exclusion site in north-east Brazil, which between 2000 and 2006 had approximately 50% of the wet season rainfall excluded. The thesis is composed of four research chapters which are independent studies prepared with the aim of submission to peer-reviewed journals and a discussion on how these research chapter relate to aims of this thesis.

This goal of this thesis is to contribute to reducing three key areas of uncertainty, discussed in the previous literature review, which contribute to reducing uncertainty in current predictions of the response of Amazonian forests to changes in climate:

- Uncertainty associated with ecological processes

- Uncertainty associated with model parameterisation
- Uncertainty associated with model structure

In Figure 1.2 we show how these key areas of uncertainty are connected to each other, relative to the goal of predicting the effect of climate change on Amazonian forests. I have orientated the titles of the four research chapters in this thesis around this diagram relative to how they target the three areas of uncertainty.

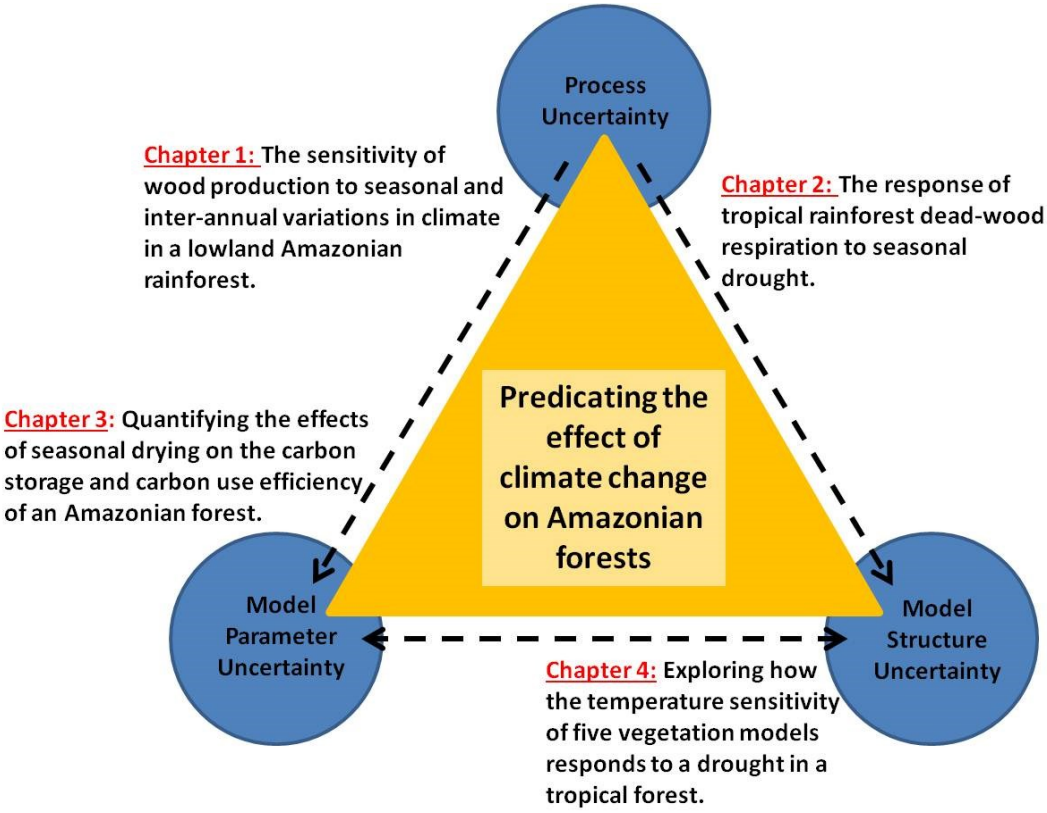

Figure1.2: A map of how the chapters of this thesis are related to three key areas of uncertainty (blue circles) and how these uncertainties are connected around the main goal of predicting the effect of climate change on Amazonian forests.

1.6.2 Chapter 2: The sensitivity of wood production to seasonal and inter-annual variations in climate in a lowland Amazonian rainforest.

In this chapter I explore how seasonal and inter-annual variations in climate influence the growth of above ground woody biomass in tropical forests. This study uses a comprehensive five-year plot-level dataset, detailing seasonal changes in woody stem increment in the lowland western Amazonian forest of Tambopata, in Peru, to assess whether seasonal change in woody stem increment can be predicted from soil moisture content or changes in other climatic variables. I also consider whether plant growth strategy (pioneer/climax) or plant functional traits (such as wood density, stem diameter and height) provide a useful basis upon which to predict seasonal changes in woody biomass.

Key Questions in Chapter 2:

1 **Are seasonal variations in woody biomass increment related to seasonal variations in water availability?**

2 **Are anomalies in soil water content and rainfall more important in controlling the rate of seasonal woody biomass accumulation than anomalies in air temperature?**

3 **Do trees with greater growth rate, diameter and height, and lower wood density experience greater seasonal variability in woody biomass accumulation?**

I find that woody biomass increment is positively correlated with the pattern of soil water content and is lowest during the dry season. Inter-annual anomalies of woody biomass increment are positively related to inter-annual anomalies in soil water content suggesting this is an important factor which restricts tree growth. However, the strength of seasonal growth patterns amongst trees is also closely related to functional traits. Consistent with a hypothesised trade-off between maximum potential growth and hydraulic safety, I find that tall and fast-growing trees had stronger seasonal growth patterns, growing more rapidly in the wet season, but being more vulnerable to water limitation in the dry season.

1.6.3 Chapter 3: The response of tropical rainforest dead-wood respiration to seasonal drought.

This chapter reports the first study of the effects of seasonal changes in water availability on the carbon dioxide released from coarse woody debris (CWD) in tropical rain forest. This study was performed at a tropical forest site in French Guiana where seasonal change in soil water availability is sufficiently strong to significantly alter both the GPP and the net ecosystem exchange. In this study I assess the influence of biotic and abiotic controls on the respiration in CWD (R_{cwd}) during the decay process. I assess the importance of this process in the context of current climate and explore ways in which seasonal changes in this carbon flux can be incorporated in to modelling studies.

Key Questions in Chapter 3:

1 **Can seasonal changes in R_{cwd} be effectively modelled using abiotic factors?**

2 **Do reductions in dry season woody tissue moisture content of CWD cause reductions in R_{cwd}?**

3 **Is the relationship between R_{cwd} and biotic factors (such as wood density and decomposition rate) altered by seasonal reductions in CWD moisture availability?**

4 **Does R_{cwd} contribute significantly to seasonal variations in ecosystem respiration?**

In this chapter I find that dry season reduction in woody tissue moisture content in CWD was responsible for reductions in the respiration flux from CWD. I find that seasonal changes in R_{cwd} can be effectively modelled using seasonal changes in soil water content, which explained 60% of the seasonal variability. I estimate that R_{cwd} is a relatively small component (5.1±0.9%) of ecosystem respiration, but under situations where CWD may increase substantially such as during land use change or other large scale mortality events, then modelling the size and climate-sensitivity of this component of the terrestrial carbon cycle is likely to become increasingly important.

1.6.4 Chapter 4: Quantifying the effects of seasonal drying on the carbon storage and carbon use efficiency of an Amazonian forest.

In this chapter I combine all the available information from seasonal measurements

of carbon pools and fluxes at a tropical forest site in French Guiana and using data assimilation I integrate this with the information provided by the structure of a carbon cycle model. This study reports how the carbon balance of this forest is altered by seasonal changes in climate and assesses with what certainty we can attribute these changes to changes in the fluxes from specific forest components. The data assimilation analysis is used to predict confidence intervals on model parameters which can provide important information on where data collection can be targeted to improve parameter constraints and reduce model uncertainty.

Key Questions in Chapter 4:

- **How does the carbon allocation to, and respiration from, the leaves, stem and roots vary between wet and dry season?**
- **Do changes in gross primary production, heterotrophic respiration or autotrophic respiration have a greater influence on seasonal changes in the carbon balance?**
- **Does the carbon use efficiency of this forest vary between wet and dry season?**

In this chapter the data assimilation analysis demonstrated that this forest sequestered four times more carbon in the dry season than in the wet season. In the dry season there were significant seasonal changes in the carbon allocation to stem and foliage, but little change in the respiration from either foliage, stems and roots. I find that reductions in heterotrophic respiration, in response to reductions in soil water content

were greater than the reductions in total ecosystem respiration, offsetting a small increase in autotrophic respiration. The data assimilation study showed that the carbon use efficiency of his forest increased from 0.35±0.02 in the wet season to 0.37±0.02 in the dry season, demonstrating that the efficiency of this forest shows little seasonal variation. The highest uncertainties in the model parameterisation were with coarse and fine root parameters, suggesting that focusing future empirical measurements on root dynamics at this site would significantly improve our current understanding of the seasonal dynamics of this system.

1.6.5 Chapter 5: Exploring how the temperature sensitivity of five vegetation models responds to a drought in a tropical forest.

In this chapter I use data from four sophisticated vegetation models to simulate the effect of a drought on a forest in the eastern Amazon using four simulated departures in atmospheric temperature from ambient 1999–2006 temperatures. This analysis explores how sensitive the leaf and canopy fluxes from each of the models are to changes in temperature, and whether the models are able to replicate the temperature responses of canopy level fluxes measured at this site. The study also explores how the temperature responses in these models are altered when a drought is also simulated.

Key Questions in Chapter 5:

1. **How sensitive to changes in air temperature are the modelled direct (biochemical) and indirect (stomatal) physiological controls on photosynthesis?**
2. **How sensitive is the modelled carbon balance of this forest to the effects of temperature change on gross primary productivity (GPP), LAI and ecosystem respiration?**
3. **Are vegetation models more sensitive to increases in air temperature or decreases in precipitation?**

In this chapter I demonstrate how all of the models simulate reduced productivity with increasing temperature and drought. However there was high variability in the sensitivity of both fluxes at the leaf and canopy scale to changes in precipitation and temperature. The models all had different sensitivities to changes in precipitation and temperature; with some more sensitive to temperature and other to drought. I demonstrate that across all the models the equivalent rise in temperature necessary to cause the same average reduction in GPP as the 50% reduction in wet season precipitation varied between 5-17.5°C. This high variability demonstrates the need for greater future constraint on model sensitivities.

1.6.6 Chapter 6: Discussion

In this chapter I synthesise the finding of this thesis and the impactions of these findings. We also suggest future work that could follow on from this research.

1.7 Chapter 7 (Appendix 1): Assessing the influence of termites on the respiration rate of coarse woody debris

1.8 Chapter 8 (Appendix 2): Canopy structure and temperature response functions in vegetation models.

1.9 Chapter 9 (Appendix 3): Co-author publications

1.10 Publication status of thesis.

Chapter 2: Re-submitted to the Journal of Ecosystems following initial revisions, November 2012.

Chapter 3: Submitted to the Journal of Ecology, November 2012

Chapter 4: To be submitted to Global Change Biology by March 2012

Chapter 5: Currently unpublished, pending further development following the receipt of data from two further vegetation models by May 2013.

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Chapter 2: The sensitivity of wood production to seasonal and interannual variations in climate in a lowland Amazonian rainforest.

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2.1 Abstract

Understanding climatic controls on tropical forest stem growth and productivity is key to developing more reliable vegetation models for predicting how tropical biomes may respond to future climate change. Currently there is no consensus on whether water availability or changes in other factors such as insolation control seasonal changes in tropical forest stem growth. This study reports the first comprehensive plot-level description of the seasonality of growth in a tropical forest, in Peru. The objectives of this study were to test how seasonal and interannual variations in climate are correlated with changes in biomass increment, and whether such relationships differ among trees with different functional traits. We find that biomass increment on the two plots was reduced by between 40 and 60 % in the peak dry season (July–September) relative to peak wet season (January–March). Inter-annual anomalies of soil water content were the only meteorological variable with a relationship with inter-annual variations of biomass increment. These results suggest that seasonal variations in growth are related to water supply. The strength of the growth seasonality response among tree species is closely related to functional traits. Thus, consistent with a hypothesised trade-off between maximum potential growth rate and hydraulic safety, tall and fast-growing trees with broad stems had the most strongly seasonal biomass accumulation, suggesting that compared to their neighbours they are more productive in the wet season but more vulnerable to water limitation in the dry season. The seasonal response of the whole forest may therefore intensify should increases in turnover and forest disturbance lead to relative increases in the populations of early successional species which are more prone to water stress.

2.2 Introduction

Tropical rainforests have the highest gross primary productivity in the world (Beer et al., 2010), yet the patterns and controls on this productivity remain quite poorly understood. Trees in tropical forests may allocate a greater proportion of their net productivity to stem growth than trees in any other biome (Malhi et al., 2011). Temporal studies of the seasonal and inter-annual variation of stem biomass increment may therefore be particularly valuable to understanding the climate sensitivity and possible shifts in the productivity of these ecosystems.

Studying seasonal changes in tropical forest function has become increasingly important in the context of developing vegetation models which simulate the correct ecological responses (Kim et al., 2012), in addition to understanding seasonal changes in productivity measured using eddy covariance data (Bonal et al., 2008, Hutyra et al., 2007, Iida et al., 2012, Carswell et al., 2002). In the absence of a present-day analogue to the climate change which is predicted to occur in the Amazon region over coming decades and centuries (Christensen et al, 2007, Cox et al., 2008, Harris et al., 2008, Marengo et al., 2012), understanding the constraints current climate poses on tropical tree growth can yield important insights to inform future predictions.

One set of studies suggests that tropical forests exhibit rapid increases in productivity and growth in the dry season when their photosynthetic rates increase in response to increased short-wave radiation (Arias et al., 2010, Clark and Clark, 1994, Graham et al., 2003, Huete et al., 2006, Saleska et al., 2003, Xiao et al., 2006). Eddy covariance data has also shown increased dry season net ecosystem productivity at some sites (Bonal et al., 2008, Hutyra et al., 2007), but not at others (Malhi et al., 1998).

Studies of seasonal tree growth increment in the tropics, however, have tended to support an alternate hypothesis of reduced growth in response to reduced water availability (Baker et al., 2003a, Chaturvedi et al., 2011, da Silva et al., 2002, Dunisch et al., 2003, Nepstad, 2002, Newbery et al., 2011, Rice et al., 2004, Wagner et al., 2012, Worbes, 1999, Clark et al., 2010). Currently, however no study has sampled the whole tree community over a sufficiently long period to capture multiple

dry seasons of different intensity. The only long term study of seasonal stem growth in tropical trees has been made on permanent forest plots in Costa Rica (Clark and Clark, 1994; Clark et al., 2010), in a forest with a wet and relatively a-seasonal climate. To date nothing is known of the seasonal patterns of stem growth in the western half of Amazonia. This in itself is a huge lacuna, given the documented strong differences in forest floristics, structure, and function across Amazonia (Baker et al., 2004, Quesada et al., 2012, ter Steege et al., 2006). Moreover, most of the ~7 million km^2 of humid forests in the neotropics are seasonal and much of this grows on soils derived from Andean sediments (Hoorn et al., 2010), yet the current generation of dynamic global vegetation models is unable to simulate the behaviour of these forests (Delbart et al., 2010).

Data from experimentally imposed drought from experiments in far eastern Amazonia have demonstrated that tree growth can be significantly reduced when soil water availability becomes limiting, particularly amongst the larger tree classes (da Costa et al., 2010, Nepstad et al., 2007). Yet, while basin-wide analysis of forest inventory data has shown a significant mortality response to natural drought events, available on-the-ground evidence for any reduction in productivity in response to drought is very weak (Phillips et al., 2009). It should be noted that the standard technique of supra-annual remeasurements to track biomass dynamics used in pan-Amazon analyses to date can be expected to have low power to detect any transient drought growth response, which occur on annual or sub annual timescales (Phillips et al., 2009). Further, water limitation can be expected to vary widely across the Amazon forest biome because of heterogeneity in soil properties (Quesada et al., 2010) and the impact this has on plant-available water (Fisher et al., 2008), and because of spatial variation in rainfall regimes (Malhi et al., 2006, Quesada et al., 2012, Marengo et al., 2012).

There is high uncertainty regarding the impact that rising atmospheric temperatures will have on the seasonal patterns of forest productivity. Some studies suggest that tropical trees are currently at the limit of their temperature threshold and that biomass accumulation rates are very sensitive to small increases in air temperature (Clark et al., 2003, Clark et al., 2010, Feeley et al., 2007). Other studies have, however,

suggested that tropical forests are not operating close to a temperature threshold and that growth is continuing to increase with rising atmospheric temperatures (Lewis et al., 2009, Lloyd and Farquhar, 2008, Phillips et al., 2008). The interacting and potentially contradictory effects of temperature, light and water availability on woody productivity and tissue metabolism, cause substantial uncertainty in our current understanding the climatic controls on tree growth and net ecosystem productivity (Meir et al., 2008). Resolving this uncertainty is important because future decreases in biomass accumulation associated with temperature rise or restricted water availability could counter the effects of recent increases in tropical forest biomass attributed provisionally to the CO_2 fertilisation effect (Lewis et al., 2009, Phillips et al., 2008); this might switch tropical forests to become a net source of carbon emissions.

The response of tree biomass increment to seasonal variations in climate will be influenced by the growth strategy of a tree, which determines biomass allocation and vulnerability to environmental stress (Chave et al., 2009, Fyllas et al., 2012, Poorter et al., 2010, Wright et al., 2010). Trait selection is often associated with a growth-mortality trade-off (Fan et al., 2012, Poorter et al., 2010, Wright et al., 2010). Investment in high wood density allows trees to create durable structures and to withstand environmental stress (Chave et al., 2009, Iida et al., 2012, King et al., 2005, Osunkoya et al., 2007, Poorter et al., 2003, Poorter et al., 2005, Poorter et al., 2010, Wright et al., 2010). Trees with low wood density sacrifice investment in strategies that reduce mortality risk in favour of rapid growth. In tropical trees this trade-off is directly related to shade tolerance (Aiba and Kohyama, 1997, Bohlman and O'Brien, 2006, Keeling and Phillips, 2007, King et al., 2005, Quesada et al., 2010, Wright et al., 2010). Therefore there is a strong functional trade-off between early successional species – low wood density, short-lived, shade-intolerant trees which invest in rapid growth to prevent mortality from shading – and late successional (climax) species, which tend to be shade tolerant, slower growing trees which invest in multiple strategies to prevent mortality, thus limiting biomass investment in growth (Baker et al., 2003b, Clark and Clark, 1994, Clark and Clark, 2001, Richards, 1996, Whitmore, 1976).

Rapid growth rates in pioneer trees necessitate increased carbon assimilation, which can be achieved through increasing the efficiency of the hydraulic system (Hacke et al., 2006, Poorter et al., 2010, Sperry et al., 2008). Increased xylem vessel diameter reduces hydraulic resistance enabling fast-growing, low wood density, tall trees to cope with the increased evapo-transpiration load associated with high-light environments and high rates of CO_2 uptake, linked to high rates of photosynthesis (Chave et al., 2009, Fan et al., 2012, McJannet et al., 2007, Poorter et al., 2010, Sperry et al., 2008). Shade-tolerant species tend to have smaller, more fibrous vessels with greater hydraulic resistance, which are much less prone to cavitation during periods of water stress (Fan et al., 2012, Hacke et al., 2006, Poorter et al., 2010, Wright et al., 2010). During periods of intense drought in the Amazon, low wood density trees apparently suffer greater mortality (Phillips et al., 2010), suggesting that wood density (as a reflection of vessel diameter) may be a good indicator of a trade-off between hydraulic efficiency and hydraulic safety.

Larger diameter trees have also been found to suffer more in periods of water stress (da Costa et al., 2010, Nepstad et al., 2007, Phillips et al., 2010), and across neotropical forests the seasonality of moisture supply is a key determinant in predicting the presence of large trees and the magnitude of stand-level above-ground biomass (Stegen et al., 2011). Taller trees have to have broader diameters to maintain mechanical stability and strength, particularly if their woody tissue is of low density (Bohlman and O'Brien, 2006, Chave et al., 2009, Osunkoya et al., 2007, Poorter et al., 2003, Poorter et al., 2010). The risk of cavitation is greater in taller trees because the necessity for wider xylem vessels, due to increased light exposure is compounded by greater hydraulic path length (Hacke et al., 2006, Poorter et al., 2010, Sperry et al., 2008). We therefore expect that taller and wider diameter trees will have the capacity for much greater growth, but will suffer greater restrictions in growth rates when water availability is limited, thus causing greater seasonal changes in biomass increment.

Previous studies of the relationships between growth rate and tree form have shown inconsistencies across trees of the same functional type (Sterck and Bongers, 1998). The observation of significant between-species variation in relative growth rate

(Baraloto et al., 2006, Chaturvedi et al., 2011, Clark and Clark, 2001, Newbery et al., 2011) suggests seasonal patterns of biomass accumulations are likely to be related to species-specific adaptations, in particular species-specific differences in the timing and duration of cambial dormancy and related metabolism (Dunisch et al., 2003). The controls on the seasonality of tropical tree biomass increment are therefore likely to be an integration of variables relating to variations in climate, functional traits and species identity.

Here we present and analyse seasonal growth data from more than five years from two research plots in western Amazonia, the longest such series (covering all trees ≥ 10 cm dbh in a plot) yet published from any seasonal tropical forest. We report quarterly (3 monthly) patterns of tree biomass increment from October 2005 to January 2011, on two 1 ha permanent forest plots, situated on contrasting soils. The aim of this study was to explore how tropical tree growth affected by reductions in seasonal changes in water availability. We test the following hypotheses:

1. Seasonal variation in woody biomass increment in this forest is related to seasonal variations in water availability.
2. Anomalies in soil water content and rainfall are more important in controlling the rate of seasonal woody biomass accumulation than anomalies in air temperature.
3. Trees with greater growth rate, diameter and height, and lower wood density experience greater seasonal variability in woody biomass accumulation.

2.3 Methods

2.3.1 Site

The study was conducted on two long-term 1 ha plots located at the Tambopata Biological Reserve, in Madre de Dios region. The two plots (TAM05 (-12°49' 49.04" S, -69°16'13.92" W) and TAM06 (-12°49'49.04" S, -69°16'13.92" W)) are

permanent sample plots of the RAINFOR network and were established in 1983 and monitored according to common protocols (http://www.geog.leeds.ac.uk/projects/rainfor/), and together span most of the edaphic variation in south-west Amazonia (Quesada et al., 2010). All trees ≥ 10cm diameter (at 1.3m or above buttressing) have been tagged and identified to species level. Sites in the western Amazon may give a better inference at the mean pattern of stem growth across the Amazon; our site has a mean precipitation (2417 mm yr^{-1}, Malhi et al.,2004) and dry season length (4-5 months, Malhi et al., (2013)) close to the mean annual precipitation for the whole of the Amazon (2138 mm yr, Galbraith et al.,(2010)) and the dry season length for a majority of the Amazon (Good et al., 2011). A summary of basic plot, climate (Malhi et al., 2004) and soil data (Quesada et al., 2010) is shown in Table 2.1.

TAM05 is situated on poorly drained relatively infertile Haplic Cambisol soil (Alumic, Hyperdystric, Clayic). In contrast TAM06 is situated on a more fertile Haplic Alisol (Hyperdystric, Siltic) and is located near the edge of the Rio La Torre. The plots have significantly different environment and vegetation; TAM05 is located on an old Pleistocene terrace with lower fertility, whereas TAM06 is located on a Holocene alluvial terrace with relatively high fertility (Anderson et al., 2009). Average wood density was higher for TAM05 (0.61 ±0.007 g cm^3) than TAM06 (0.49±0.007 g cm^3). Palm trees were much more common for TAM06, where 30.1% (118) of the stems were palm trees; in contrast only 3.7% (18) of the stems for TAM05 were palm trees. As palms have low wood density and generally do not have large diameter stems they only accounted for 1.5% of the total biomass for TAM05 and 11.6% of the biomass for TAM06. Structural differences could have significant

effects on the seasonal patterns in biomass accumulation and so the data for the two plots were analysed separately.

Table 2.1: Summary of plot, climate, soils and leaf data for Tambopata plots. Plot level biomass values are calculated from 2011 census data downloaded from forestplots.net (Lopez-Gonzalez, Lopez-Gonzalez et al., 2011) using biomass equations from Feldpausch et al., (2011) and wood density from the global wood density database (Chave et al., 2009; Zanne et al., 2009). Mean annual rainfall and mean annual temperature (MAT) are average values from 1960–1998 used in Malhi et al., 2004. Soil data are taken from Quesada et al., (2009).

	TAM05	**TAM06**
2011 Biomass (Mg ha^{-1})	262.3	298.2
Stem Count	563	699
Rainfall mm yr^{-1}	2417	2417
MAT (*˚C*)	25.2	25.2
Soil Type	Haplic Cambisol (Alumic,Hyperdystric, Clayic)	Haplic Alisol (Hyperdystric, Siltic)
Soil Sand (%)	39.76	2.43
Soil Clay (%)	43.53	45.66
Soil Silt (%)	16.71	51.91
Soil N (%)	0.16	0.17

2.3.2 Meteorological data

Solar radiation, air temperature, relative humidity and precipitation time series were collected from an automatic weather station (AWS) in a clearing near TAM-06 (12.84°S,69.29°W). The original data were measured with a 30 minute resolution for

the period March 2005 to December 2011. These data were quality controlled to remove outliers and then averaged into monthly values. Monthly mean values with <90% of the monthly data existed were discarded and gap-filled. Solar radiation was gap-filled using mean monthly values from other years of data. Mean daily temperature valuesa, which includes daytime and night-time values, were gap-filled using daily values from a nearby SENAMHI (Peruvian Meteorological Service) station at Puerto Maldonado (12.58°S, 69.20°W). Values from SENAMHI station were regressed against daily values from the AWS to correct for the differences between the stations. The corrected values from SENAMHI were used to gap-fill the temperature data. Average night time temperature data were gap-filled using adjusted 07.00 (local time) temperatures from the SENAMHI station where available. Any remaining gaps in average night time temperature were filled by subtracting the mean monthly night-time and daily temperature difference from months in other years from the mean daily difference in temperature.

Too few values for relative humidity were available from the AWS therefore, the more complete time series from the SENAMHI station was substituted. The precipitation time series was gap-filled using values from the SENAMHI station at 07.00 and 19.00 (local time) which were aggregated to produce monthly estimates. If fewer than the maximum possible number of daily values were available, the month was considered to be missing. Where these data were missing, monthly values from the nearest grid point of the TRMM (Tropical Rainfall Measuring Mission) 3B43 product were used.

The cumulative water deficit (CWD) is the difference between rainfall and evapo-

transpiration, assuming evapo-transpiration from canopies in the Amazon is 100 mm a month, as has been found from studies using empirical measurements, and model estimation (Fisher et al., 2009, Shuttleworth, 1989). It is a measure of the water stress in tropical forests and was calculated using the methodology described in Aragão et al. (2007). The methodology for soil water content (0-30cm depth) data collection is reported in Malhi et al. (2013). Monthly meteorological, CWD and SWC data were averaged to quarterly means to match the period of dendrometer increments.

2.3.3 Dendrometer measurements

From April 2005 to January 2011 dendrometers were installed and measured at 1.3m height, on all trees ≥ 10cm diameter at breast height (dbh), unless the stem of the tree was buttressed, in which case the dendrometer was installed above the buttresses. Prior to installation of the dendrometers in April 2005, the diameter of all the trees was measured using a diameter tape. From April 2005 stem increments were measured from the dendrometers every three months at the start of January, April, July and October. During the first 3-12 months after dendrometer installation stem increments can be underestimated as dendrometers go through an adjustment period (da Silva et al., 2002, Keeland and Sharitz, 1993). We found that the first two increment intervals, April to June 2005 and July to September 2005, underestimated stem increments relative to subsequent periods and therefore we excluded the first six months of measurements. From October 2005 to January 2011, we conducted 23 quarterly censuses of the dendrometers.

Diameters measured from dendrometer were converted to biomass estimates using a

tropical moist forest biomass equation, which used tree height, tree diameter and wood density (Chave et al., 2005). Tree height was measured using a laser range-finder for all trees ≥ 10cm diameter at breast height (1.3m), on both plots, once in 2005 by JSE. For the purposes of this study we assume height to be constant over the period of this study, and consequently the biomass accumulation results only reflect stem diameter growth. Wood density was estimated based on the Global Wood Density Database (Zanne et al., 2009), available online at http://datadryad.org/repo/handle/10255/dryad.235). The equation from Chave et al. (2005) was used with the diameter measurements to calculate the biomass of each tree every three months. The biomass of palm trees was calculated as the volume of a cylinder. To distinguish growth patterns from patterns of tree mortality and recruitment, only trees which were alive and at least 10cm diameter from April 2005 to January 2011 were included in our growth calculations.

2.3.4 Correcting errors

Large positive or negative spikes in the increment pattern of a stem are characteristic of errors which occurred during dendrometer measurement. Removing such errors is important to eliminate bias in plot level biomass increments. For each tree, identified errors were corrected by replacing the increment error with the mean increment from the same quarterly period in the other available years. In total 394 increments were corrected, accounting for less than 1.5 % of all of the measured tree increment data points used in this study.

As large negative growth rates are unlikely to result from bole shrinkage, all negative

growth increments below the 2 standard deviations from the mean negative growth increment from all trees were corrected. Following this a screening process was performed, whereby trees' increment data were plotted if the minimum increment was < -0.1 cm and the difference between the minimum and mean increment >3 standard deviations from the mean negative increment for a specified tree. Plotted increment data were then visually assessed to confirm that the detected error was real and not a result of a repeated growth pattern. If the minimum increment was identified as an error, it was corrected. This screening process was repeated three times to catch repeat errors in the data and to re-check previously uncorrected data.

To eliminate errors associated with over-estimates from dendrometer bands trees' increment data with a maximum increment greater than 0.1cm and where the difference between the maximum and the mean increment was > 3 standard deviations. As with the negative spike screening, plotted data were visually assessed to confirm that the detected positive growth 'spike' was uncharacteristic of the growth pattern of the tree. If a spike was confirmed to be uncharacteristic, the value was corrected. As above, this data screening was repeated three times.

Following the removal of errors from the data, a factor to compensate water-induced changes in stem diameter was subtracted from all trees. During dry periods, when relative humidity is lower, desiccation of tree bark and changes in tree water use in tropical trees can cause significant reductions in diameter (Baker et al., 2002, Stahl et al., 2010). To account for the gain and reduction in incremental growth associated with changes in stem water retention bole shrinkage was estimated for each quarterly period from the mean negative growth pattern in trees which showed no overall

growth (n=192). To account for the impact of shrinkage on our estimates, this shrinkage term was applied to all trees. If the degree of seasonal shrinkage is correlated with growth rates (see below), this correction would underestimate the correction required for faster growing trees.

2.3.5 Pioneer Index

A Pioneer Index was compiled and analysed by one of us (OP) using independent sources to determine the degree of consensus that the species is a pioneer, applying the 'informant consensus' principle used in sociological and ethnobotanical literature (e.g. Adu-Tutu et al., (1979); Phillips and Gentry (1993)), scoring each taxon according to the consensus of opinions expressed by experts. Our four independent sources consisted of three experts in the ecology of the Peruvian Amazon flora (Rodolfo Vásquez, Abel Monteaguado, and OP), and one literature source, the information compiled from thousands of voucher collections from Peru by L. Brako and J. Zaruchi (Brako and Zarucchi, 1993). Species were defined as type 1 pioneers if known/reported to colonize large gaps in primary forests, and as type 2 pioneers if predominant in early secondary forest, roadsides, riverbanks, and other human-disturbed areas. Each taxon was scored by each source as one of two states: 0 (non-pioneer), or 1 (pioneer), for each of the two types, and the mean derived for that particular taxon-expert combination. Each taxon's consensus score was then computed as the un-weighted mean across experts (i.e., sum of these average values attributed by experts, divided by the number of experts consulted), the Index therefore varying on a continuous scale between 0 and 1.

2.3.6 Statistical analysis

All statistical analyses were carried out in the statistical package R (R 2.14.2, R-project software, http://www.r-project.org R 2.14.2) and all errors are reported as the standard error of the mean. Where propagation of errors was necessary this was done by quadrature (Aragão et al., 2009, Malhi et al., 2009). Single linear correlations were performed between all meteorological and soil water content data and mean quarterly biomass increment for each plot. Correlating biomass increment with the available meteorological and SWC drivers does not necessitate any causal relationships between abiotic variables and tree biomass increment. To explore possible causal relationships further, we also examined interannual anomalies in the seasonal growth rates, to assess how deviations from a mean state of a variable impacted deviation from mean patterns of tree biomass increment. Anomalies for each of the five meteorological variables (CWD, PPT, T, SWR, RH), the SWC from each plot and for the total biomass increments for TAM05 & TAM06 were created. We considered the anomaly to be the value for each of the quarterly intervals, minus the mean value for that quarterly period over all years (2005–2011). To assess how deviations from the mean seasonal pattern of biomass increment was related to deviations from the mean seasonal pattern of meteorological drivers a principle components analysis was performed with the mean quarterly anomalies of biomass increment and meteorological data available for each plot over the whole period (soil water content was therefore excluded as only available from 2007).

To assess how seasonal the relative biomass accumulation per tree was we employed

a normalised seasonality index (SI). An SI was created for each complete year of measurements (four measurements per year) for all trees. SI was calculated using equation 1, where BI_{dry} and BI_{wet} are the biomass increment in peak dry season (July–September), and peak wet season (January–March) of a given year, for a given tree and BI_{max} is the maximum seasonal growth rate recorded for that tree.

$$SI = \frac{BI_{dry} - BI_{wet}}{BI_{max}} \qquad \textit{Equation 1}$$

To assess the effects of inter-specific variations in the seasonality of biomass accumulation an analysis of variance was performed (ANOVA) for genera with greater than 10 individuals. As species diversity is high this analysis was performed at the genus level rather than the species level to enable sufficient sample size.

2.4 Results

2.4.1 Stem and biomass distributions

For TAM05 and TAM06, respectively 66.8% and 59.9% of stems are in the smallest size class, while 40.8 % and 47.0 % of the respective biomass resides in trees of the largest size class, which have a great mean biomass increment (Figure 2.1). The unequal distribution of biomass and stem counts across stem size classes was not reflected in the distribution of total biomass increment, which was much more evenly distributed across stem size classes (Figure 2.1). The mean biomass increment from

non-palm trees (dicots) for TAM05 and TAM06 combined was significantly correlated with both stem diameter (r^2=0.37, p<0.001) and height (r^2=0.49, p=0) when plotted on a $\log_{10}$ scale (data not shown). No significant correlation was found between the mean biomass increment of palms and stem diameter or height.

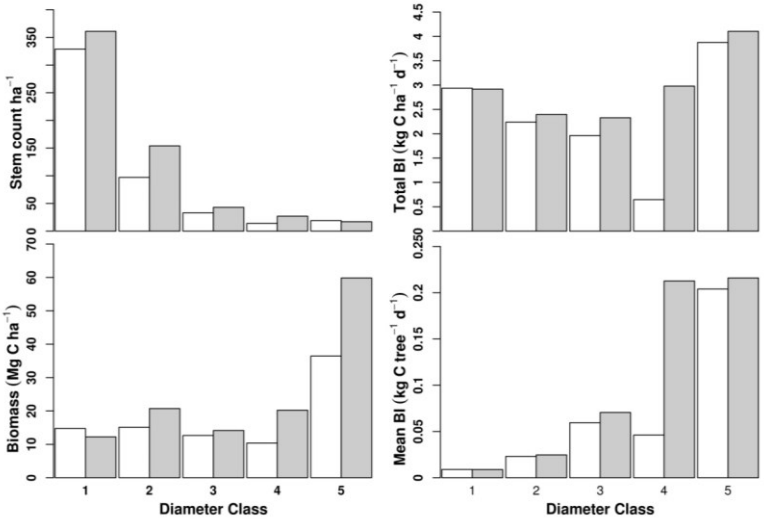

Figure 2.1: Stem counts (stems ha-1, top left panel), total biomass (Mg C ha-1, bottom left panel), total biomass increment (BI; kg C ha-1 d-1; top right panel), and mean biomass increment (kg C tree-1 d-1) for different wood diameter classes (D, cm; 1: 10<D≤20, 2: 20<D≤30, 3: 30<D≤40, 4: 40<D≤50, 5: D>50) for TAM05 (white bars) and TAM06 (grey

2.4.2 Seasonal variations in meteorology

Mean monthly rainfall over the study period showed a consistent seasonal pattern, peaking in January at 375±34 mm month^{-1} and falling to 28±8 mm month^{-1} in August (Figure 2.2). Mean monthly temperature showed no consistent seasonal pattern; average mean monthly temperature was 24.6±0.1ºC. Monthly relative humidity and short-wave radiation showed slight seasonality; between February and August relative humidity dropped from 87.9±1.1 to 79.8±1.0%, and short-wave radiation

increased from 140.0±7.5 to 162.0±2.7 W m^{-2} $month^{-1}$ (Figure 2.2). From 2007–2010 soil water content (SWC, m^3 m^{-3}) averaged 19.4±1.3 m^3 m^{-3} in TAM05 (the sandier site) and 32.6±2.9 m^3 m^{-3} in TAM06. The maximum difference in soil water was between peak wet season (January–March) and peak dry season (July–September) intervals (Figure 2.3); soil water content varied by 45.1±10.5% in TAM05, and by 53.3±14.6% in TAM06 between peak wet and dry season.

2.4.3 Seasonal variations in biomass increment

Biomass increment was 39.7±12.0 % and 58.3±11.8 % lower respectively for TAM05 and TAM06 in peak dry season (July–September) than in peak wet season (January–March; Figure 2.3). Mean dry season biomass increment was similar between TAM05 and TAM06 (Figure 2.3, mean difference = 1.1±11.0 %); however, during peak wet season stand level biomass increment was 31.7±12.76 % lower in TAM05 than in TAM06.

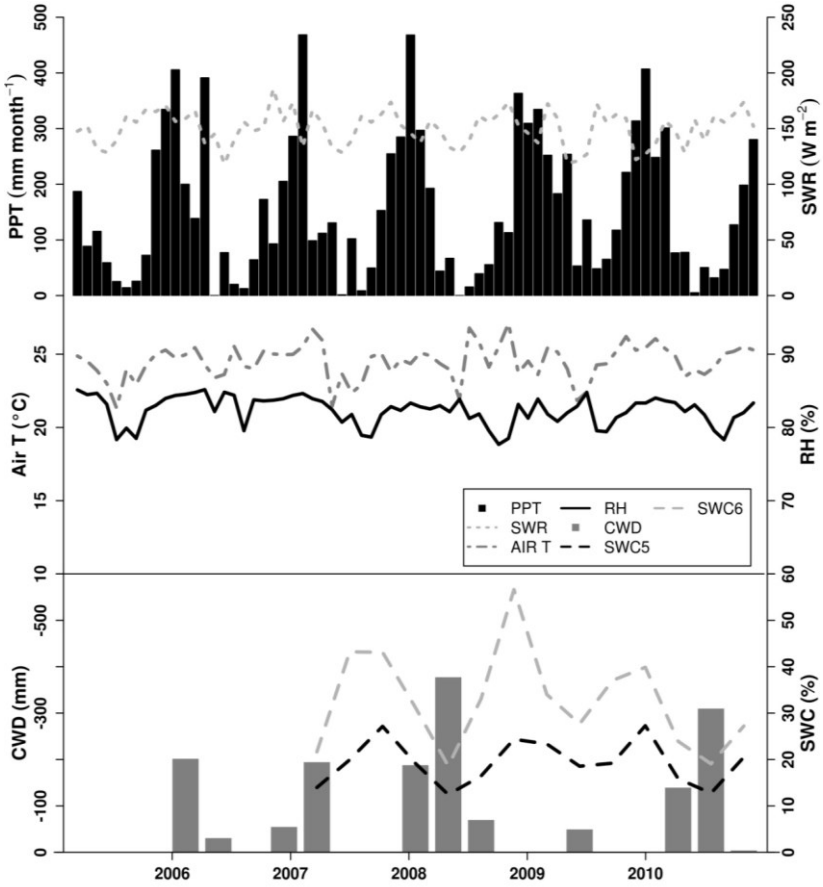

Figure 2.2: Monthly meteorological data. Top Panel: Monthly precipitation (PPT, mm month-1, black bars) and monthly mean short-wave radiation (SWR, W m-2, dashed grey line). Middle Panel: Monthly mean air temperature (Air T, °C; dashed grey line) and monthly mean relative humidity (RH, %; black line). Lower Panel: Cumulative water deficit (CWD, mm, grey bars), volumetric soil water content for TAM05 (SWC5, %, black dashed line) and TAM06 (SWC6, %, grey dashed line).

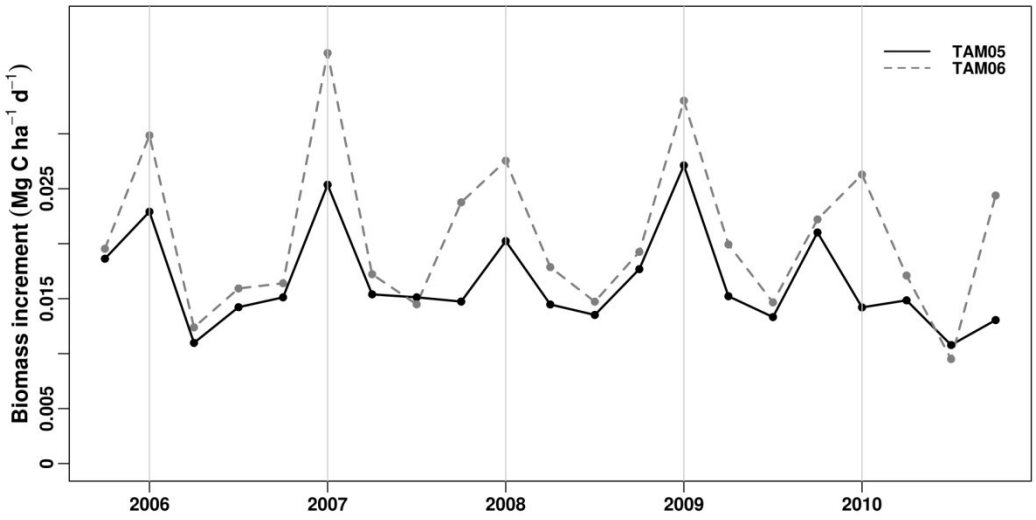

Figure 2.3: The mean quarterly biomass increment (Mg C ha^{-1} day^{-1}) for all trees for TAM05 (solid black line) and TAM06 (dashed grey line. Vertical lined divide the graph into annual periods.

Strong seasonal patterns in the meteorological drivers, particularly precipitation and SWC, resulted in highly significant correlations between these variables and the biomass increment on the two plots (Figures 2.3 and 2.4, Table 2.2). The mean quarterly biomass increments on each plot was positively linearly correlated with the seasonal patterns of precipitation, CWD, and mean night-time temperature and, for TAM06, also with relative humidity, mean daily temperature and soil water content (Table 2.2). However, anomalies of precipitation and relative humidity showed no correlation with anomalies of biomass increment; anomalies of soil water content (SWC) had significant and CWD weak correlations with anomalies of biomass increment but only for TAM06 (Table 2.2). Anomalies of mean air temperature were not significantly correlated with anomalies of biomass increment on both TAM05 and TAM06. Analysis of variance tests on multiple regression analysis demonstrated that no combination of anomaly variables significantly improved the strongest single correlation with biomass increment anomaly on either plot. The same linear correlations between meteorological data and biomass increments were performed excluding the biomass increments of palm trees from both plots and correlation to approximately the same levels of significance were obtained.

2.4.4 Interannual variation in biomass increment

We next consider the year-to-year anomalies in growth rate, once the mean seasonal cycle is factored out. The variability in the biomass increment anomaly relative to the anomalies in meteorological drivers shows a different orientation in the PCA analysis between plots (Figure 2.4). The biomass increment anomaly for TAM05 shows no

strong alignment with factors relating to water availability; in contrast the biomass increment anomaly for TAM06 shows a strong positive alignment with anomalies of precipitation and CWD suggesting greater sensitivity to soil moisture deficit (Figure 2.4). Biomass increment anomaly was negatively orientated to mean daily and night-time temperatures (Figure 2.4), however no significant correlations were found between these variables (Table 2.2). For both plots the primary axis of the PCA analysis explained <45 % and the secondary axis <25 % of the variability in the data. Consistent with the results of the linear regressions, this suggests that a substantial amount of the variability in the data remains unexplained by the variables presented in this analysis.

*Table 2.2: r^2 values from linear relationships between the mean quarterly biomass increment and mean quarterly values for 6 climatic variables from October 2005 - January 2011 (soil water content data from July 2007 - January 2011). Correlations between biomass increment for TAM05 (BI_TAM05) and TAM 06 (BI_TAM06; Mg C ha-1 day-1) and: maximum cumulative water deficit (CWD, mm), precipitation (PPT, mm day-1), average daily air temperature (T, °C), average night-time air temperature (TN°C), relative humidity (RH, %), and volumetric soil water content (SWC, %) are shown in the first two columns of correlations. In the second two columns the results of correlations of anomalies in quarterly biomass increment for TAM05 (BI_a_TAM05), and TAM06 (BI_a_TAM06) with the anomalies in the met drivers (indicated by '_a' appended to above abbreviations) are shown. The * symbol indicated the relationship is significant at ≤0.1, ** indicates significance at ≤0.05 and *** indicated significance at ≤0.01.*

	BI_TAM05	**BI_TAM06**	**BI_a_TAM0**	**BI__a_TAM0**
CWD/CWD_	0.230**	0.354***	0.015	0.145*
PPT/PPT_a	0.449***	0.677***	-0.006	0.029
T/T_a	0.130	0.229**	-0.039	-0.043
TN/TN_a	0.260**	0.371**	-0.008	0.000
SWR/SWR_a	0.090*	0.054	0.025	-0.020
RH/RH_a	0.152	0.278**	0.005	0.108
SWC/SWC_a	0.229	0.699***	0.021	0.490***

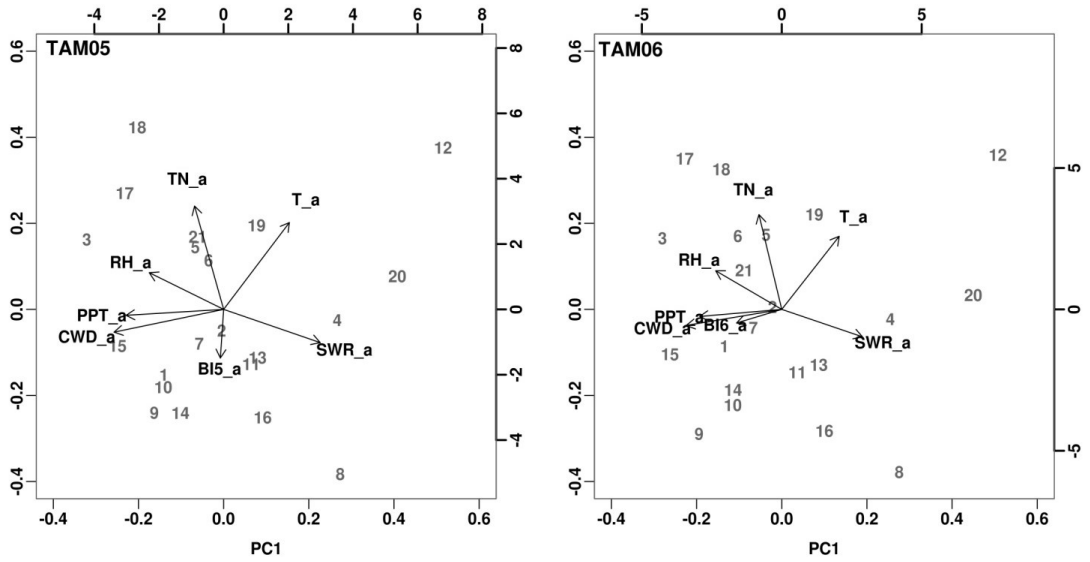

Figure 2.4: Results of a principle components analysis (PCA) between anomalies mean of quarterly biomass increment (BI) for TAM05 (left panel, BI5_a) and TAM06 (right panel, BI6_a) and the anomalies of maximum cumulative water deficit (CWD_a, mm), precipitation (PPT_a, mm day-1), air temperature (T_a, °C), night-time air temperature (TN_a, °C), relative humidity (RH_a, %) and short wave radiation SWR_a. Numbers indicate the score of each quarterly period from October 2005 to January 2011 on the two main principle components and the arrows indicate the loading of each variable onto the two principle components. Principle component 1 (PC1) explained 42.3% of the variability for TAM05 and 44.39% of the variability for TAM06. Principle component 2 (PC2) explained 23.5% of the variability in the data for TAM05 and 22.7% of the variability in the data for TAM06. As Cadis negative a positive correlation with CWD indicates decreasing water stress.

2.4.5 Seasonality index and its relationship to tree structure and density

The mean seasonality index (SI) in non-palm trees was negative on both plots (TAM05 SI = -0.02±0.02, TAM06 SI= -0.10±0.02); hence most trees show less growth in the dry season. SI values for trees for TAM06 were significantly more negative than trees for TAM05 (Welch two sample t-test, p=0.004), showing these trees had a greater relative wet season growth (or less relative dry season growth). When (non-palm) trees from TAM05 and TAM06 were grouped, high wood density

trees on average exhibited almost no seasonality in growth, whereas low wood density trees had strong reductions in growth in the dry season. This results was represented in the increase of SI from -0.19±0.04 to -0.03±0.03 when wood density class increased from 0.2–0.4 g cm^2 to ≥0.7 g cm^2 (Figure 2.5b).

Seasonality index was -0.07±0.04 for 10–20cm diameter trees, increasing to -0.22±0.03 for 30–40cm diameter trees (Figure 2.5a). This relationship did not hold for trees ≥50cm diameter which had a mean SI of -0.10±0.04. Hence, in all but the largest trees, seasonal reductions in stem growth increased with stem diameter. The most extreme declines in SI were observed with increases in tree height class and biomass increment. Shorter trees on average showed no seasonality (SI = -0.03±0.04) in growth, but large trees show large dry season reductions in growth rate (SI = 0.24±0.04; Figure 2.5c). Similarly SI decreased from 0.02±0.04 in trees with the low biomass increments (≤ 0.0125 Mg C ha^{-1} day^{-1}) to -0.27±0.03 in trees with high biomass increment (≥0.1 Mg C ha^{-1} day^{-1} Figure 2.5d), showing faster growing trees experienced greater decreases in dry season growth.

Surprisingly, there appeared to be no relationship between SI and succession status, as represented by the Pioneer Index (r^2=0.005, p=0.03, Figure 2.5e). However, for 16 genera for TAM05 and 13 genera for TAM06 which had more than 10 individuals, an analysis of variance test showed that there were significant variations in the mean SI between genera. (TAM05, p=<0.001; TAM06 p=<0.001).

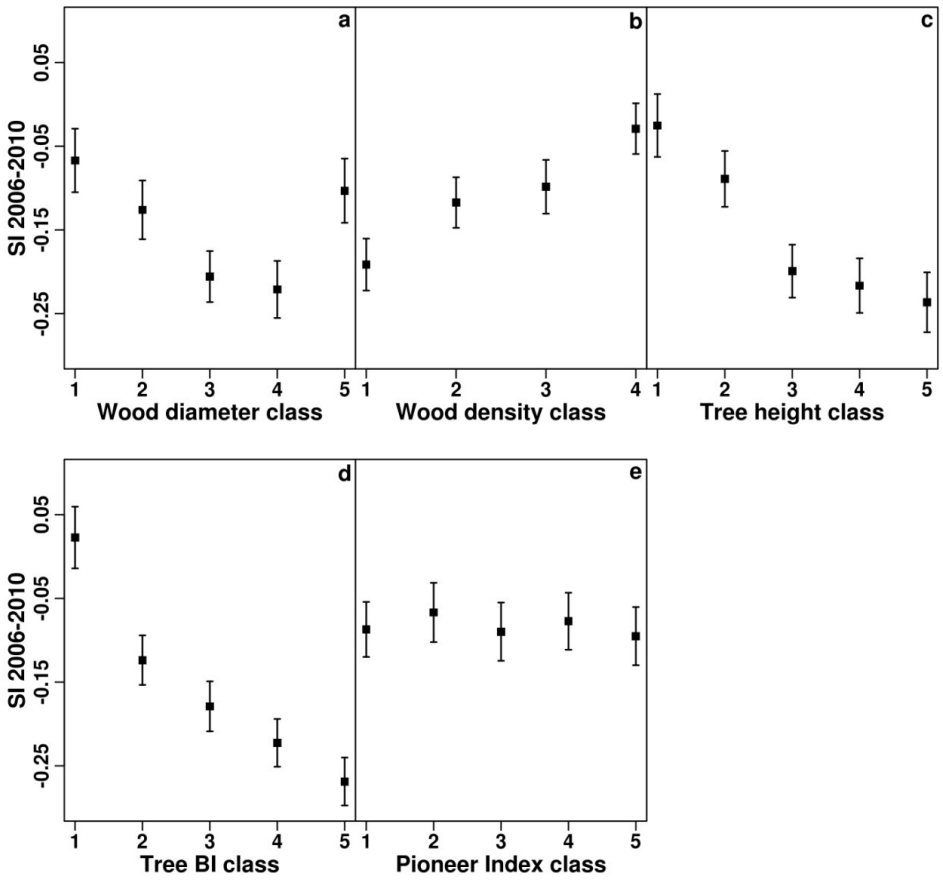

Figure 2.5: Mean 2006–2010 seasonality index (SI) for non-palm trees from both plots of different diameter, wood density and height classes. a: Mean SI and standard error for trees of different wood diameter classes (D, cm; 1: 10<D≤20, 2: 20<D≤30, 3: 30<D≤40, 4: 40<D≤50, 5: D>50). b: Mean SI and standard error for trees of different wood density classes (WD g cm^{-3}; 1: 0.2<WD≤0.4, 2: 0.4<WD≤0.55, 3: 0.55<WD≤0.7cm, 4: D>0.7). c: Mean SI and standard error for trees of different tree height classes (H m; 1: H>10, 2: 10<H≤20, 3: 20<H≤30, 4: 30<H≤40 , 5:H>40). d: Mean SI and standard error for trees of different mean tree biomass increment classes (BI (Mg C ha^{-1} day^{-1}) 1: BI≥0.0125, 2: 0.0125< BI ≤0.025, 3: 0.025< BI ≤0.05, 4: 0.05< BI ≤0.1 5: BI ≤0.1). e: Mean SI and standard error for trees of different pioneer index classes (PI, 1: PI≥0.001, 2: 0.001<PI≤0.2, 3: 0.2<PI≤0.3, 4: 0.3<PI≤0.4: PI≤0.4). A negative SI indicates that trees grow less in the dry season (Jul-Sep) compared to the wet season (Jan-Mar).

2.5 Discussion:

Over a period of more than 5 years, diameter increments from all trees ≥ 10cm diameter on two 1 ha plots reveal very strong seasonality (Figure 2.3). The reduced growth rate on both plots was positively correlated with dry season reductions in precipitation and SWC (Figure 2.2, Table 2.2). The period of highest stem growth (mid wet season) does not correspond to the periods of greatest leaf productivity associated with changes in phenology (the end of the dry season; Malhi et al., (2013)). Patterns of stem growth are therefore more strongly associated with seasonal changes in water availability than seasonal patterns of maximum rate of leaf productivity, confirming hypothesis one that seasonal variation in woody biomass increment in this forest is related to seasonal variations in water availability.

Our study suggests that the strength of the positive effect of intra-annual variability in soil water availability on intra-annual variability in tree biomass increments reported by others (Chaturvedi et al., 2011, Wagner et al., 2012) could be related to functional adaptations to soil conditions. Consistent with these studies we find SWC was also a very strong predictor of quarterly biomass increment, but only for TAM06 (Table 2.2). Stem biomass increment for TAM05 was significantly related to precipitation and CWD, but, in contrast to TAM06, had no relationship to SWC (Table 2.2). TAM05, which had sandier soils, had a lower annual mean SWC, and we therefore hypothesise that the trees on this plot may be more adapted to coping with reduced water availability.

However, as with growth seasonality in temperate forest ecosystems, it is possible that the seasonal patterns of growth are synchronised with the climate seasonality,

rather than being immediately driven by them. Hence the correlations with seasonal factors may provide little information about the longer-term response of forests to changes in environmental conditions. The analysis of anomalies across years, on the other hand, may provide some evidence of some direct physiological responses to environmental variability. Hence it is not surprising that the anomaly correlation analysis identifies as significant environmental variables that differ from those identified using the seasonal correlation analysis (Table 2.2).

Although the soil water content data were only available for part of the dataset (July 2007 onwards), the data show that, on both plots, years with the lowest dry season SWC (2008, 2010; Figure 2.2) has the lowest biomass increments (Figure 2.3). Correlations with anomalies demonstrated that anomalies of SWC were a strong correlate with anomalies of biomass increment (explaining almost 50% of the variability) for TAM06. We speculate that the anomalies of SWC are correlate with anomalies of biomass TAM06 but not TAM05 because TAM06 experiences higher SWC values and therefore the trees have adapted to higher SWC and are more restricted by the greater oscillation in SWC on this plot (Figure 2.2). In contrast the SWC remains significantly lower in the wet season on TAM05, suggesting these trees may have become more adapted to drier conditions, and therefore may be less affected by oscillation in SWC.

Anomalies of biomass increment for TAM06 were positively orientated with anomalies of precipitation and CWD in the PCA plot (Figure 2.4). Anomalies of cumulative water deficit (CWD) also showed a weak positive correlation with anomalies of biomass increment for TAM06. This result suggests that higher/lower-

than-average plant available water causes higher/lower-than-average quarterly stand level biomass accumulation. This is however only the case for TAM06 which, despite having greater mean annual soil moisture content, has a greater seasonal shift in soil water content (Figure 2.2).

Anomalies of quarterly mean daily and night-time temperature had a negative orientation with biomass increment anomaly for TAM05 (Figure 2.4); however we found no significant correlations between these variables in the linear regressions (Table 2.2). Therefore for this forest we find no significant evidence to support the findings of Clark et al. (2003; 2010) and Feeley et al., (2010) who find growth rates respond negatively to increasing temperatures. Therefore we accept hypothesis two that anomalies in SWC and rainfall are more important in controlling the rate of seasonal woody biomass accumulation than anomalies in air temperature.

We find hypothesis three, which stated trees with greater growth rate, diameter and height, and lower wood density would experience greater seasonal variability in woody biomass accumulation, to be true. Relative differences in biomass accumulation between the dry and wet season amongst trees is related to wood density, stem diameter, height and average biomass increment (Figure 2.5). Although no direct correlations were found, we see a strong positive trend between mean SI by wood density class and a negative trend between mean SI by height and stem diameter (Figure 2.5).

This supports the theory of growth-mortality trade-off. Fast-growing lower wood density trees tend to grow taller to avoid shading (Aiba and Kohyama, 1997, Chave et al., 2009, Keeling and Phillips, 2007, King et al., 2005), and with increasing

vertical extension these trees tend to display more rapid diameter expansion to maintain mechanical stability (Bohlman and O'Brien, 2006, Iida et al., 2012, Osunkoya et al., 2007, Poorter et al., 2003, Poorter et al., 2005), and high rates of photosynthesis and water demand. The prioritisation of large vessel size does, however, make these trees more prone to environmental stress caused by reduced water availability (Fan et al., 2012, Poorter et al., 2010, Wright et al., 2010). Taller, fast-growing, light-demanding pioneer trees have a higher transpiration load, enabling enhanced production in high-light environments and perpetuating greater growth when there is sufficient water available (Fan et al., 2012, McJannet et al., 2007, Poorter et al., 2010, Sperry et al., 2008, Wright et al., 2010). However, increased hydraulic and productive efficiency in these trees necessitates wider xylem vessels, which puts them at much greater risk of cavitation when soil water content is restricted (Fan et al., 2012, Poorter et al., 2010, Sperry et al., 2008, Wright et al., 2010). Average wood density, which shows an inverse relationship to vessel diameter (Sperry et al., 2008), was significantly lower for TAM06 (0.49±0.007 g cm^3) than for TAM05 (0.61 ±0.007 g cm^3). It is therefore possible that the greater abundance of narrow vessel, high wood density trees on TAM05 causes the relationship between anomalies of SWC and biomass increment not to be apparent on this plot.

Taller trees, in particular, are at greater risk to cavitation because they have longer hydraulic path lengths (Poorter et al., 2010). To avoid cavitation when water availability is restricted, trees with wide xylem vessels have to shut their stomata, thus restricting maximum photosynthetic rates. Our data were consistent with this interpretation where tall, fast-growing, low wood density trees had significantly

greater growth rates in the wet relative to the dry season; this produces the observed more negative SI. Our findings are also consistent with those observational and experimental drought studies in the Amazonia and elsewhere in the tropics, which report that taller trees with lower wood density are at an elevated risk of mortality from restricted water availability (da Costa et al., 2010, Nepstad et al., 2007, Phillips et al., 2010, Meir and Woodward, 2010).

Decreasing SI with increasing diameter is only observed in trees up to 40cm dbh and trees with a dbh ≥50cm have an SI more similar to that observed in trees of 10–30cm dbh (Figure 2.5a). In mature forests the very largest trees may be the slow-growing species which over long periods of time out-compete fast-growing pioneers (Baker et al., 2003b, Clark and Clark, 1992, Clark and Clark, 2001, Richards, 1996, Whitmore, 1976). We would not expect these trees to have the same hydraulic trade-off as observed in the low wood density trees, which develop broad stems to support rapid vertical growth (Osunkoya et al., 2007), and therefore this may partly explain why the very largest trees do not have the lowest SI.

We find significant differences in the SI among genera ($p<0.001$) and these variations do not seem to be related to pioneer –climax functional group differences (Figure 2.5e). Other tropical studies have found that there are significant differences between the relative growth rates of different species (Baker et al., 2003b, Baraloto et al., 2006, Chaturvedi et al., 2011, Clark and Clark, 1992, Clark and Clark, 2001, Dunisch et al., 2003, Newbery et al., 2011). It appears that species-specific growth adaptations may therefore generate significant noise about the observed relationships between functional groupings, such as wood density, diameter, height, and growth

rate, and seasonality of biomass. Similarly it is likely that inter-specific variations in growth rates will also be contributing to the variance within observed functional groups. Despite intra and inter-specific noise, the presence, abundance and range of different functional groups are clearly important controls on how tree biomass increment responds to seasonal shifts in climate and therefore this forest could acclimate functionally to current and future changes in temperature and water availability through selective pressures on trees with certain functional traits.

2.6 Conclusion

This study presents, to our knowledge, the first comprehensive plot-level description of the seasonality of growth in a tropical forest over several years. At this study site we found that stand level biomass accumulation on the two study plots decreased by ~40% and 60% in peak dry season, relative to peak wet season. The seasonal patterns of biomass accumulation are strongly associated with seasonal patterns of rainfall, light and water supply, but such seasonal variation may reflect timing and synchrony of seasonal cycles rather than direct physiological controls on tree growth rates. Cumulative water deficit (precipitation minus evapo-transpiration), and in particular soil water content, appear to be important controls on intra-annual patterns of biomass accumulation.

Furthermore, we demonstrate that there is a strong association between tree functional properties and the degree of seasonality of growth. This study is consistent with the notion that important growth-hydraulic limitation trade-offs exist among species. We find fast growing, low wood density, tall, and broad-diameter trees tend

to suffer greater restrictions in dry season productivity relative to wet season productivity, suggesting that, although they have the capability for greater growth in wet season conditions, they are at greater risk of hydraulic stress, reduced growth and possibly mortality as soil water availability drops. This group of trees is therefore more seasonal in is growth characteristics where rainfall is also seasonal. These results support the hypothesis that the functioning and species composition of forests could acclimate to current and future changes in climate through selective pressures on trees with contrasting functional traits.

2.7 Acknowledgements

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Chapter 3: The response of tropical rainforest dead wood respiration to seasonal drought

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LR: Study design, data collection, data analysis, paper writing. CS: Project design, data collection, and contribution to paper writing. DB: Study design, and contribution to paper writing. MW: Study design, and contribution to paper writing. LS: Contribution to methods, data analysis. PM: Study design, and contribution to paper writing

3.1 Abstract:

Coarse woody debris (CWD, dead wood sections ≥ 10 cm diameter) represents a large store of carbon in tropical forests; however estimates of the flux of carbon from CWD in these forests remain poorly constrained. The objective of this study was to resolve the dry/wet season response of respiration in CWD (R_{cwd}), and investigate the importance of biotic and abiotic factors for predicting the seasonal change of R_{cwd} at the ecosystem level. This study presents a four-month time series of R_{cwd} measurements conducted on 42 dead trees (26 species) at the Paracou Research Station in French Guiana. R_{cwd} measurements were repeated 13 times on each CWD sample from July to November 2011, spanning the transition from wet to dry season, and then from dry season to the following wet season. Seasonal drought caused monthly R_{cwd} to drop by 20.5±5.1 % over the wet-dry transition. Changes in woody tissue moisture content explained 41.9 % of the measured seasonal variability in R_{cwd}, but 60 % of the seasonal variability in mean forest R_{cwd} rates could be modelled using surface soil water content. We conclude that seasonal variations in R_{cwd} contribute appreciably to seasonal variations of R_{eco}, and should be included in functional models simulating the response of tropical rainforest ecosystems to current and future climate.

3.2 Introduction:

The Amazon forest is one of the planet's largest terrestrial carbon stores and in a global context, Amazonia has one of the highest levels of gross primary production (Beer et al., 2010). The undisturbed forest in recent years has generally been considered to be a net carbon sink (Chambers et al., 2004; Lewis et al., 2009; Malhi et al., 2009b), however recent analysis suggests it may now be a source of atmospheric carbon (Gloor et al., 2012). The longevity and resilience of a sink, or the change to a source, are all uncertain, partly because both photosynthesis and respiration are differentially sensitive to climate change and because longer term ecological responses to climate change, such as tree mortality, remain difficult to quantify (Meir and Woodward, 2010; McDowell, 2011). To understand potential future shifts in the Amazon carbon balance, we need to improve our understanding of how ecosystem respiration and photosynthesis will respond to changes in environmental conditions, and possibly the least well documented are the responses to climate by different respiring components in these forest ecosystems (Meir et al., 2008).

Coarse woody debris (CWD) in tropical forests is one such understudied carbon pool (Chambers et al., 2000; Chambers et al., 2001; Keller et al., 2004; Baker et al., 2007; Hutyra et al., 2007). CWD has been defined as all dead woody material >10 cm in diameter (Chambers et al., 2000); estimates of the mass of the CWD pool in tropical forests are uncertain and currently reported values vary from forests with no estimates of CWD to forests with up to 83 Mg C ha^{-1} (Baker et al., 2007). CWD in Amazonian forests is estimated to contain 12.7 % of the carbon stored in above-

ground woody biomass (Chao et al., 2009), but in some Amazonian forests this value has been found to be >30 % (Clark et al., 2002; Rice et al., 2004; Baker et al., 2007; Chao et al., 2009). There are known methodological pitfalls associated with measuring CWD dynamics (Chao et al., 2009) and hence our understanding of CWD and its vulnerability to changes in climate or other drivers currently carries much uncertainty across scales, from plot to region (Clark et al., 2002; Keller et al., 2004; Wilcke et al., 2005; Chao et al., 2009).

Over 75% of CWD carbon loss is through respiration (Chambers et al., 2001); the remaining CWD carbon is lost through fragmentation, biological transformation, leaching, and weathering (Mackensen et al., 2003). Quantifying the factors which control CWD respiration is key to understanding the changes in the magnitude of the CWD pool. CWD respiration is caused by multiple decomposer communities, which convert CWD carbon to carbon dioxide (CO_2) via respiration. The overall process is complex, and influenced by interactions of multiple biotic and abiotic agents, causing high temporal and spatial variability. This complexity potentially makes CWD respiration difficult to understand and quantify, unless one or a few primary controls on the process can be identified.

The moisture content of CWD, and the meteorological variables which control it, such as vapour pressure deficit (VPD), soil water content (SWC), and precipitation, are likely to limit respiration rates in CWD (Harmon et al., 1986). Moisture content of CWD has been shown to have a positive relationship with both CWD decay (mass loss) and respiration (R_{cwd}) across both temperate and tropical forests (Chambers et al., 2000; Chambers et al., 2001; Torres and Gonzalez, 2005; Jomura et al., 2007;

Forrester et al., 2012). Low available moisture limits the activity of decomposers, particularly fungi (Cornwell et al., 2009; Weedon et al., 2009). Moisture content in CWD has been shown to influence the variability of R_{cwd} between CWD samples in the tropics (Chambers et al., 2001), but to our knowledge there is no information on how temporal changes in R_{cwd} are controlled by temporal changes in CWD moisture content. Similarly the relationships between the influence of abiotic controls, such as moisture and temperature, and biotic factors, such as wood density, chemistry, diameter, and stage of decomposition remain poorly understood. Biotic factors are known to influence how susceptible CWD is to attack from decomposers (Harmon et al., 1986; Martius, 1997; Chambers et al., 2001; Keller et al., 2004; Zhou et al., 2007; Beets et al., 2008; Cornwell et al., 2009; Weedon et al., 2009; Hérault et al., 2010; van Geffen et al., 2010). If abiotic factors have a strong influence on the relationships between biotic controls and R_{cwd}, abiotic factors may provide a simpler predictive tool for modelling ecosystem level R_{cwd} responses to drought. Recent severe Amazonian drought events (Marengo et al., 2008; Marengo et al., 2011) significantly increased tree mortality rates, and therefore also increased the volume of CWD across the Amazon (Phillips et al., 2009; Phillips et al., 2010); suggesting that any future drought events (Christensen et al, 2007; Cox et al., 2008; Harris et al., 2008) may, at least transiently, enhance the role of CWD in the terrestrial carbon cycle in this region. Exploring the best way to model the seasonal responses of R_{cwd} is therefore important because it provides a mechanism to make first approximations of the impact of drought on R_{cwd} at the ecosystem level.

This study was conducted at the Paracou research station in French Guiana, a tropical rainforest site which experiences strong seasonal changes in rainfall and soil

moisture availability (Bonal et al., 2008; Wagner et al., 2011). Reductions in stem and soil respiration have already been shown to coincide with reductions in ecosystem respiration at the site (Bonal et al., 2008; Stahl et al., 2011), although currently the contribution of R_{cwd} to reductions in R_{eco} remains unknown. The aim of this study is to investigate the impact of seasonal changes in environmental conditions on R_{cwd}. Our aim was to test the following hypotheses:

1 Reduced dry season woody tissue moisture content of CWD will cause reductions in $R_{cwd.}$

2 Relationships between R_{cwd} rates and biotic factors alter seasonal reductions in CWD moisture availability.

3 Seasonal changes in R_{cwd} flux in tropical rainforests can be effectively modelled using metrics of temperature and moisture alone.

4 R_{cwd} significantly contributes to seasonal variations in ecosystem respiration.

3.3 Material and Methods

3.3.1 Site

The study was conducted at the Paracou Research Station, French Guiana (5°16'43''N, 52°55'28"W). The vegetation is a tropical lowland rainforest and the ten year average rainfall at the site is 3041 mm per year (Gourlet-Fleury et al., 2004), with significant changes in seasonal rainfall caused by the movement of the Inter-Tropical Convergence Zone to the north and south of the country. There is a long wet

season from December to July sometimes interrupted by a short dry period in March and a long dry season from August to November, when rainfall is often reduced to <50 mm a month (Bonal et al., 2008). The study was conducted on two 70 by 70 m *terra firme* forest plots at 40 m above sea level. The plots were adjacent, on the same soil type, nutrient poor acrisol soils (FAO-ISRIC_ISSS 1998), and had similar biotic characteristics (Table 3.1). CWD samples were examined from both plots to maximize sample size. Annual gross primary production for the forest was estimated to be 37.4 Mg C ha^{-1} yr^{-1}, and annual R_{eco} was 35.8 Mg C ha^{-1} yr^{-1}, in 2004-2005, suggesting the forest is a small carbon sink (Bonal et al., 2008).

Table 3.1: Plot characteristics from the two 70 m x 70 m study plots: species diversity measured in 2010 (species number per plot), stem density measured in 2010 (stems ha^{-1}), litter-fall (2004-2009 average, Mg $ha^{-1}yr^{-1}$), and leaf area index (LAI, m^2 m^{-2}) measured in September 2011.

Plot	Species density	Stem density	Litterfall	LAI
GX1	103	612	7.28±0.39	5.46±0.38
GX9	116	755	6.42±0.30	7.01±0.20

3.3.2 Sampling strategy

Bi-annual (every 2 years) tree census data starting in 2004 were used to identify stem mortality on both plots since this date. The subsequent field survey identified 42 mortality events from which CWD samples from 26 species were selected. The samples were selected to cover a range of periods (2004-2010), living wood specific gravity (WSG, 0.46-0.97) the density of wood relative to the density of water

(Williamson and Wiemann, 2010), and tree trunk diameters (10.5-105.0 cm). We divided CWD into two classes: CWD in contact with the ground, those woody sections that had fallen and were in contact with the ground (n=24) and CWD with no contact with the ground (i.e. standing or fallen but suspended off the ground; n=18). CWD without contact with the ground had, on average, 36.2±0.1 % drier woody surface moisture (WSM) at the end of wet season (28/07/2011) and 52.4±0.1 % drier WSM at the end of dry season (07/10/2011). The contact and non-contact CWD subgroups were used to test if seasonal changes in R_{cwd} were different in CWD which was usually drier. Although dead branches >10 cm diameter are included in our definition of CWD, the measurements made in this study only include dead tree stems, standing or fallen, to link closely to the census data. Diameter was determined using large callipers placed around the CWD boles.

3.3.3 Respiration measurements

The fluxes of CO_2 from CWD were measured 13 times over the period 28 July 2011 to 15 November 2011, a period which captured a wet-dry-wet transition in 2011 (Figure 3.1). A week prior to the first measurement, each piece of CWD was brushed gently to remove any surface moss, which photosynthesises and therefore may alter respiration values. Red paint was used to mark the CWD 20 cm either side of the measurement point on each sample tree bole to ensure that repeated measurements were taken in the same place. Diurnal variability studies of R_{cwd} showed there to be no significant diurnal pattern in R_{cwd} (data not shown). Attempts were still made however, to measure the CWD samples in the same order to minimize any

undetected effects of time of day on the change in R_{cwd}.

Instantaneous CO_2 flux measurements were made with a PP Systems EGM4 infra-red gas analyser (PP Systems, Hitchin, UK), using the closed-dynamic chamber method. The EGM4 was connected in a closed loop to a clear Perspex chamber (0.375 m^3) containing a small fan to mix the air inside the chamber. The chamber was sealed to each piece of CWD using a rubber sealant (Terostat-VII, Teroson, Ludwigsburg, Germany) and an adjustable strap to hold the chamber securely to each piece of CWD. Once the chamber was sealed to the CWD the rate of CO_2 accumulation was measured for 220 seconds. Before the measurement period commenced, the chamber was flushed through a re-sealable opening to ensure that measurements started with CO_2 concentration in the chamber close to atmospheric levels (400-500 ppm at the forest floor). The first 100 seconds of measurement was considered an equilibration period, and the CO_2 records from the 100-220 second period were first examined for linearity and then used to calculate the rate of CO_2 accumulation in the chamber using linear regression (Stahl et al., 2011). A temperature probe attached to the EGM4 (STP-1 Soil Temperature Probe, Hitchin, UK) was placed next to the chamber to simultaneously measure the CWD surface temperature. The chamber was tested for leaks by blowing around the edges of the chamber. Measurements where the linear regression of CO_2 accumulation with time had an $r^2<0.99$ were then discarded from the analysis, to ensure that no data in which there was a possible leak was included. The CO_2 efflux rate from each piece of CWD was then determined with Equation 1 using the change in CO_2 concentration over the change in time ($\Delta CO_2/ \Delta t$), the chamber volume (Vch, l) and surface area (Sch, m^2), the volume of a mole of CO_2 (Vol.mol) and the CWD temperature (Tcwd, °C).

Respiration was not temperature corrected because variation in CWD temperature was too small (mean surface wood temperature was 27.2±0.1 °C) to detect a relationship between R_{cwd} and CWD temperature (data not shown).

$$R_{cwd} = \left(\frac{\Delta CO_2}{\Delta t}\right) * \left(\frac{Vch}{Sch}\right) * vol.mol * \left(\frac{273}{273+Tcwd}\right) \qquad \textit{Equation 1}$$

Mean R_{cwd} per measurement period and mean woody surface moisture per measurement period refer to the mean respiration and CWD moisture values calculated for each of the 13 measurement periods, respectively. These mean values were only calculated from a set of 33 CWD samples for which a successful measure was taken in every measurement period. Mean R_{cwd} per sample and mean woody surface moisture per sample were calculated from measurements taken across all measurement periods, for each of the 42 CWD samples.

3.3.4 CWD moisture measurements

Directly following each R_{cwd} measurement a wood surface moisture sensor (Dampmaster, Laserliner, London, UK) was used to estimate wood surface moisture (WSM) at four points within 10 cm of each CWD sample point. The moisture sensor was used to give an index of woody tissue moisture content from 1 to 100 based on the electrical conductivity between two electrodes, which were inserted ~1 cm into the surface of the CWD. The conductivity measures are sensitive to the wood density

of each sample and to correct for this, after the last campaign, a small wood sample was cut from the surface of each piece of CWD to calibrate the sensor. Each sample of CWD was weighed and then dried to constant mass and re-weighed to determine the original moisture content as a percentage of dry mass. This gave a specific calibration for each CWD sample for the final campaign. These calibrations were applied to the measurements of woody tissue moisture content from all previous campaigns, assuming a linear response of the sensor moisture measurements to CWD moisture of each sample.

3.3.5 Wood specific gravity and wood chemistry

After the last measurement campaign a wood section (~10-20 cm thick) was removed from the chamber location on each piece of CWD. This section was photographed and, where still remaining, samples from the bark, sap and heartwood were taken from each piece of excised tissue to measure the wood specific gravity (WSG) in the current decayed state. Due to the difficulties associated with defining the boundary between sap and heartwood we assumed that the active xylem closest to the point underneath the bark was sapwood and the wood at the centre of the section was heartwood. On the same day each sample was placed in water in a sealed plastic bag and hydrated for 2 days. Water-saturated mass was then measured and the volume of the woody section determined by water volume displacement. The woody section was then dried to constant mass at 105 °C for 2 days, and the dry mass of the sample was determined. Bark, sap and heart WSG (unitless) was then calculated using the CWD sample dry mass (dM, g), and CWD sample saturated volume (sV,

cm^3) relative to the density of water (ρwater, 1 g cm^{-3}) (Equation 2; see Williamson and Wiemann (2010)).

$$WSG = \frac{dM}{sV.\rho water} \qquad \textit{Equation 2}$$

ImageJ software (http://rsbweb.nih.gov/ij/) was used to calculate the area of the cut surface and, where we were able to determine boundaries between wood types, what fraction of this area was bark, sap and heart wood. Mean WSG was then calculated using average bark, sap and heart WSG, weighted by fractional surface area.

An interior and exterior sample of the CWD was taken for chemical analysis of C, N, cellulose, hemi-cellulose and lignin content that was conducted at the Cell Wall Laboratories, University of Edinburgh. The interior samples were taken from the closest point to the centre of the radial sections, representing the heartwood. The external samples were taken from the sapwood closest to the surface of the radial sections, representing sapwood. Lignin content was assayed by the acetyl bromide method (Hatfield and Fukushima, 2005), assuming specific absorbance of lignin=0.17. Hemicelluloses were assayed by acid hydrolysis (incubated in 2 M TFA at 120°C for 1 hr) followed by PAHBAH assay for monosaccharides (Hatfield and Fukushima, 2005). It was assumed that 15 mg hemicellulose yields 18 mg glucose equivalents of reducing sugars (Hatfield and Fukushima, 2005). Cellulose was assayed by the anthrone method on TFA-insoluble material (Hatfield and Fukushima, 2005). C and N were determined at the University of Edinburgh using a Carlo Erba NA2500 Elemental Analyser.

3.3.6 Fractional mass remaining

Fractional mass remaining (FMR) is the fraction of the original mass of a CWD sample at the time of death which remains at present. Hérault et al. (2010) found that the FMR of CWD at Paracou could be calculated using living WSG, living circumference and time since death with an r^2 of 0.6. Living circumference and time since death, taken from tree inventory data, and living WSG, taken from Rutishauser et al. (2010), were used to calculate the fractional mass remaining for each sample (see *Equation 1*, Table 2 in Hérault et al 2010).

3.3.7 Meteorological data and ecosystem respiration

Vapour pressure deficit (VPD, kPa) and air temperature below the forest canopy (2 m above the ground) and precipitation above the canopy were measured every 30 minutes during the measurement period; equipment and methods are described in Bonal et al (2008). Daily soil water content (SWC, m^3 m^{-3}) was measured at 10 cm depth; 13 gaps (one single day gap and one gap of 12 days) in the SWC data for 2011 were filled by linear interpolation (Bonal et al. 2008). Precipitation, VPD, SWC and air temperature were averaged into weekly means to quantify mean climate conditions prior to the measurement and to explore correlations with mean R_{cwd} and WSM per measurement period. Net ecosystem exchange (NEE) measurements were measured taken from an eddy covariance tower<100m from our study site. The NEE data was processed as described in Bonal et al., (2008) and used to estimate annual R_{eco} using the method of Reichstein et al (2005) (Siebicke, unpublished data).

3.3.8 Spatial and diurnal variability studies

To assess patterns of radial and longitudinal variation in R_{cwd} in fallen tree trunks, detailed measurements of spatial variability were made on 5 CWD samples from the two study plots (n=5). For each sample stem, four measurements of R_{cwd} were made at ~1 m intervals down the trunk, starting from the point of measurement used in the main (temporal) experiment. Three radial R_{cwd} measurements were then made, starting at the point of measurement and then at ~75° and 150°, where 180° was the central point of the bole facing or touching the ground.

Diurnal measurements of R_{cwd} were carried out to test for daily variability in R_{cwd} on 3 separate days (26/07/2011, 09/08/2011 and 23/11/2011). Because of the logistical difficulty of making diurnal measurements *in situ*, these data were taken at a small research forest site located at the research centre in Kourou, 50 km from the field site. In total 13 separate pieces of CWD were measured using the same methodology and equipment used for measuring R_{cwd} in the field, as described above. Samples were selected to cover a range of states of decay, assessed visually and according to night-time accessibility. R_{cwd} was measured from each sample every 2 to 3 hours from 6 am until 10 pm, i.e. at the time of the day when air temperature variations are the greatest. 5 of the 13 samples measured on the 26 July had repeat diurnal measurements done on 09 August, to confirm the initial findings that had suggested no diurnal pattern. No significant patterns were detected in either the spatial or the diurnal R_{cwd} pilot studies, and therefore spatial and diurnal variations in R_{cwd} are considered to follow a random distribution by frequency and deviance from the

mean.

3.3.9 Statistical analysis

All statistical analyses were carried out in the statistical package R (R 2.14.2, R-project software, http://www.r-project.org R 2.14.2). The data for R_{cwd} and WSM had skewed distributions so these data were log-transformed and all correlation analyses used the log-transformed data sets. Autocorrelation (ACF) and partial autocorrelation analysis (PCF) showed there was no autocorrelation or moving average components in the R_{cwd} and WSM data of each tree. Linear and non-linear models were compared using analysis of variance tests (ANOVA) and the Akaike's information criterion (AIC). Stepwise regression in both directions was used to determine the best multiple linear regression model based on the AIC output. To test for lagged responses the meteorological drivers were correlated as weekly averages or sums of 1, 2, 3 and 4 weeks prior to the measurement day. Jtests (lmtest package, R) were performed to statistically compare non-nested linear models of correlations between mean R_{cwd} per measurement period and the meteorological drivers lagged by different numbers of weeks.

To assess if the relationships between the sample variability in R_{cwd} rates and WSM, and biotic factors, such as FMR, WSG, wood chemistry, and diameter changed seasonally, the coefficient of determination (r^2) value from relationships calculated for each measurement period was plotted against the mean woody surface moisture for each campaign. This provided a test of whether there was a seasonal pattern to the strength of the relationship between biotic factors and sample variability in R_{cwd}.

3.3.10 Plot-level scaling

CWD respiration measurements were scaled to plot level using inventory data from a 6.25 ha permanent undisturbed sample plot situated <100 m from our study plots and on the same soil type (Gourlet-Fleury et al., 2004). This plot was selected over our study plots because plot censuses used to track input from stem mortality into the CWD fraction were available from 1991, and this long period allowed total CWD stocks to be better estimated. The biomass of every piece of CWD, at the point of death (the biomass of the tree as it died), was calculated for 1991 to 2011 using the biomass equation for moist tropical forests in Chave et al. (2005). This equation uses: tree diameter, which was calculated from the census data; tree height, which was calculated using the tree height equation calibrated to forests in Guiana Shield Amazonian forest (see table A2 in (Feldpausch et al., 2011)); and wood density, which was taken from Rutishauser et al. (2010).

The current biomass of all pieces of CWD which had died since 1991 was determined by calculating the fraction of the initial biomass which remained for each piece of CWD. The fractional mass remaining (FMR) was calculated using the equation from Hérault et al. (2010), using the circumference, WSG at the point of death and time of death of the CWD as model inputs. Stems with an FMR that was less than 1.0 % were excluded, assuming that CWD decayed to this level are likely to be incorporated into the soil. Total CWD biomass was calculated for the end of 2011. To estimate R_{cwd} at a plot level, estimates of R_{cwd} were multiplied by the total CWD biomass.

3.4 Results

3.4.1 Climate

Over the experimental period there was a large reduction in rainfall from 203.2 mm per month in July to a minimum of 23.6 mm per month in September (Figure 3.1). In 2011 the rainy season started unusually early with the heavy rains starting at the end of October (Figure 3.1). There was no significant change in weekly average temperature over this period (Figure 3.1). Reductions in mean weekly rainfall were linked to reductions in mean weekly soil water content (r^2=0.36, p=0.005) and increases in weekly mean VPD (r^2=0.60, p=<0.001; also see Figure 3.1).

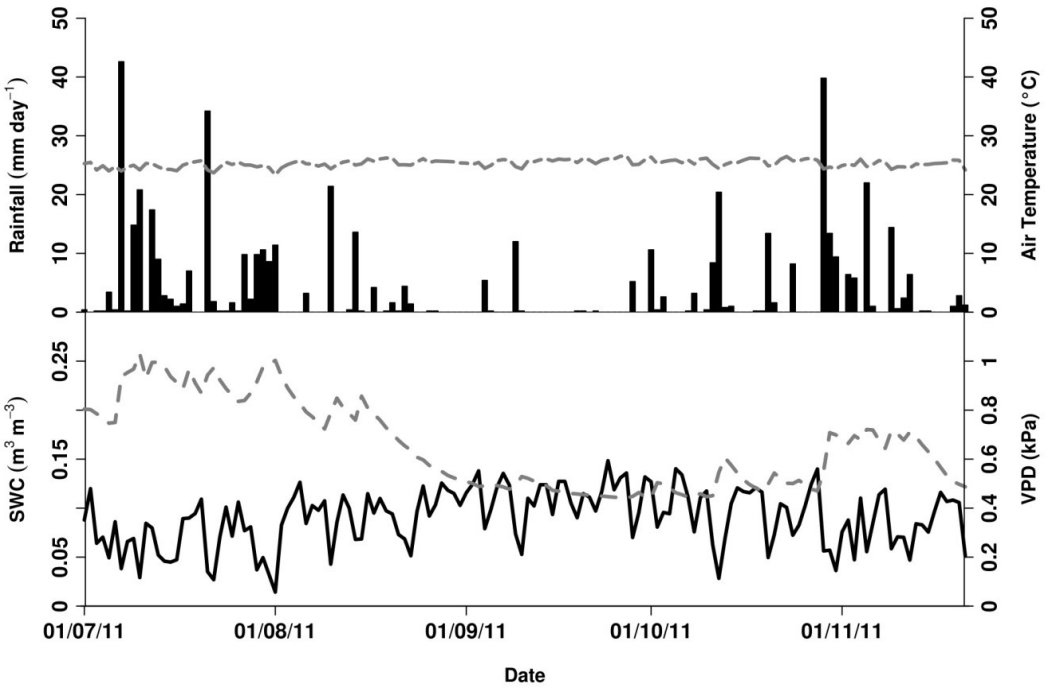

Figure 3.1: Meteorological data for June 2011 to December 2011. Top Panel: precipitation (black bars, mm day^{-1}) and mean daily temperature below the forest canopy (grey dashed line, °C). Lower Panel: SWC (grey dashed line, m^3 m^{-3}) and mean daily VPD (black line, kPa) (lower panel).

3.4.2 The impacts of seasonal drought on R_{cwd}

Mean WSM fell from 0.90±0.14 g H_2O g dry mass^{-1} at the end of the wet season (28th July) to 0.56±0.08 g H_2O dry mass^{-1} on the 7th of October, just before the wet season started, a reduction of 38.2 % (Figure 3.2). Mean WSM then returned close to pre-dry season levels towards the end of October, after a period of heavy rains (Figure 3.2). From the end of July to the first week in October mean R_{cwd} decreased from 0.14±0.02 to 0.09 ±0.01 mg C g^{-1} d^{-1}, a reduction of 35.6±9.8 % (Figure 3.2*)*. From October to late November, the period during which the wet season began, R_{cwd} recovered, increasing by 33.3 ±9.8 %. Mean $\log_{10}$ WSM per measurement period was significantly positively correlated with mean $\log_{10}$ R_{cwd} per measurement period (r^2=0.42, p=0.001, Figure 3.3). This relationship was steeper and most significant (r^2=0.65, p=0.001) in CWD samples with no soil contact, and was not significant in CWD with soil contact, which had higher respiration and WSM values (Figure 3.3*)*. At the end of the wet season (28th of July) CWD with soil contact had mean WSM and R_{cwd} 32.2±0.08 % and 56.2±0.04 % greater, respectively, than CWD samples with no soil contact. At the end of dry season (7th of October) this difference increased to 52.4 % and 60.7 %, respectively.

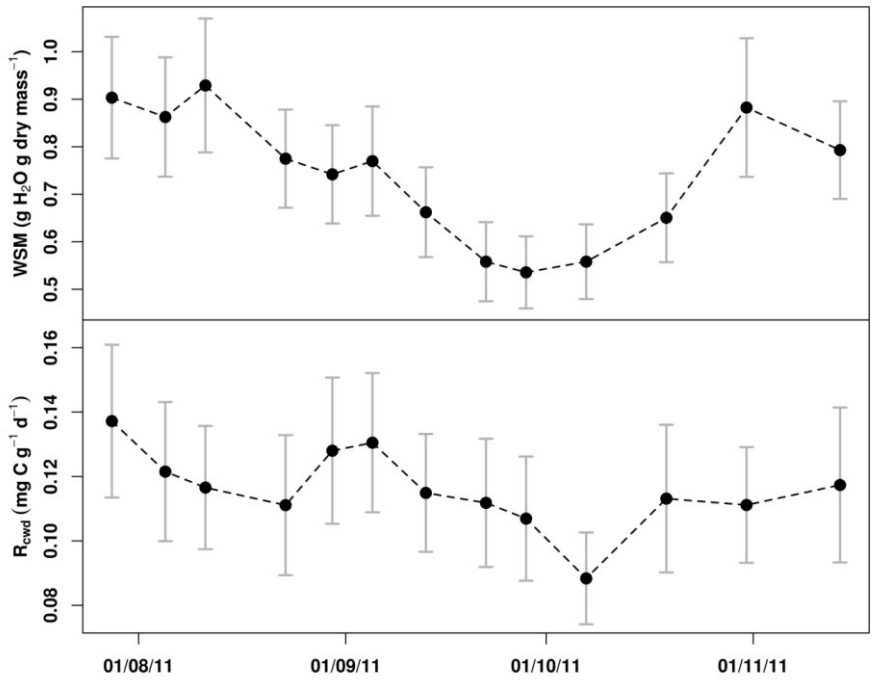

Figure 3.2: Mean wood surface moisture per measurement period (g H_2O g dry mass^{-1}, upper panel) and mean R_{cwd} per measurement period (mg C g d^{-1}, lower panel). Grey bars show the standard error, (n=33).

Mean surface wood temperature was 27.2±0.1 °C. There was no relationship between surface temperature and log10 $R_{cwd,}$ even using data from all measurement periods (n=526). A temperature response was lacking presumably because 97.3 % of all of the temperature measurements were between a narrow temperature range (24 and 30 °C, data not shown).

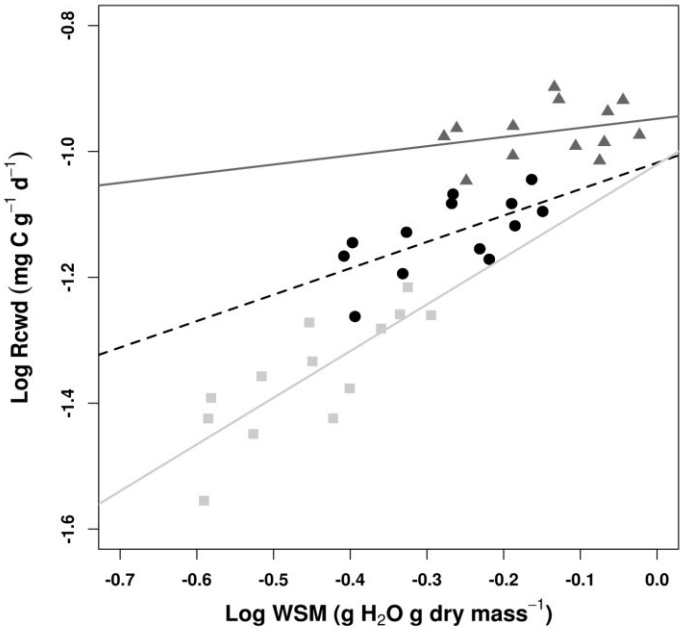

Figure 3.3: Linear relationships of the mean log_{10} R_{cwd} per measurement period (mg C g d^{-1}) and the mean log_{10} wood surface moisture per campaign (WSM, g H_2O g dry $mass^{-1}$). Black circles and dotted black line indicate the mean R_{cwd} of each measurement period (n=33, r^2= 0.42, p=0.001). Dark grey triangles and dark grey line indicate the R_{cwd} of each measurement period for CWD with forest floor contact (n=19, r^2=0.09, p=0.329). Light grey triangles and light grey line indicate the R_{cwd} of each measurement period for CWD with no forest floor contact (n=14, r^2= 0.65, p=0.001).

Average weekly SWC was significantly correlated with mean $\log_{10}$ R_{cwd} per measurement period when lagged by 2, 3 and 4 weeks, even though the strongest correlation (r^2=0.60, p=0.002) was found using a 3 week lag (i.e. soil moisture 3 weeks prior to the R_{cwd} measurement day; Table 3.2). A lag of 3 weeks also produced the strongest correlation between mean $\log_{10}$ R_{cwd} per measurement period and average weekly VPD (Table 3.2). No correlation was found with mean $\log_{10}$ R_{cwd} and precipitation.

SWC lagged by 3 weeks was found to be the best model for estimating seasonal changes in R_{cwd}; analysis using ANOVA demonstrated that a linear model combining the strongest lagged correlations of VPD and SWC, and mean $\log_{10}$ WSM did not significantly improve the model for predicting mean $\log_{10}$ R_{cwd} per measurement period (p=0.86).

*Table 3.2: Shows the correlation of determination (r^2) and significance value (p) for linear correlations of mean weekly VPD (kPa), weekly precipitation (mm) and mean weekly SWC (m^3 m^{-3}) with the mean log_{10} R_{cwd} per measurement period (μg C g^{-1} hr^{-1}) 1, 2, 3 and 4 weeks prior to the measurement campaign. Grey boxes indicate the strongest significant correlation. Jtests were performed sequentially with the strongest correlations and subsequent strongest correlations to test for significant differences and * indicates the strongest lagged correlations were significantly best at the >0.95% confidence level, or the other lagged correlations it was equally significant with.*

	1 week prior		***2 week prior***		***3 week prior***		***4 week prior***	
Correlation	***r^2***	***P***	***r^2***	***p***	***r^2***	***p***	***r^2***	***p***
VPD vs R_{cwd}	**0.11**	0.274	**0.37***	0.028	**0.48***	0.009	**0.19**	0.137
Precipitation vs R_{cwd}	**0.02**	0.646	**0.05**	0.449	**0.21**	0.118	**0.28**	0.061
SWC vs R_{cwd}	**0.28**	0.065	**0.38**	0.025	**0.60***	0.002	**0.42**	0.017

3.4.3 Inter sample R_{cwd} variability

Mean $\log_{10}$ WSM per sample significantly affected the variability of mean $\log_{10}$ R_{cwd} per sample, as well as the seasonal signal. Mean $\log_{10}$ WSM and $\log_{10}$ R_{cwd} per sample were significantly positively correlated (r^2= 0.31, p<0.001, Figure 3.4*)*. When R_{cwd} and WSM were correlated for all samples within each period, the 13 correlation of determination values (r^2 values) showed a negative asymptotic relation with the mean WSM for each campaign ((y=a+(b-a)*exp(-exp(c)/x), Figure 3.5). In drier conditions CWD moisture apparently determined more of the variation in R_{cwd} among different CWD pieces; the r^2 dropped sharply once plot-level mean WSM rose above 0.8 g H_2O g dry mass^{-1}.

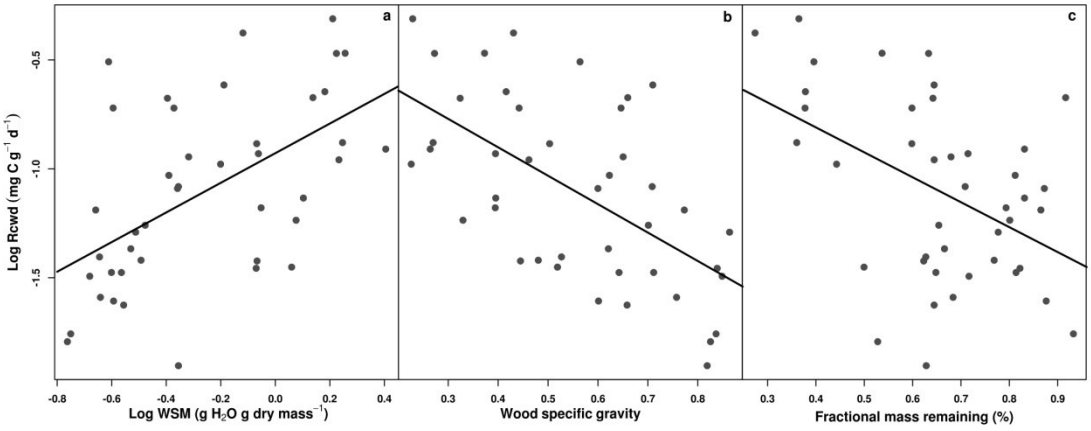

Figure 3.4: Linear correlations of mean log_{10} sample R_{cwd} (mg C g d^{-1}) against log_{10} sample wood surface moisture content (g H_2O g dry mass^{-1}, a, r^2=0.31, p<0.001), sample wood specific gravity (WSG, b, r^2=0.36, p<0.001), and sample fractional mass remaining (FMR, %, c, r^2=0.21, p=0.002).

Mean $\log_{10}$ WSG explained 36 % of the variability of the mean $\log_{10}$ R_{cwd} between samples ($r^{2=}0.36$, $p<0.001$, Figure 3.4). WSG and WSM were negatively correlated with each other ($r^{2=}0.47$, $p=0.001$). Diameter, living wood density, and time of death showed no correlation with R_{cwd} per sample. Fractional mass remaining of CWD (FMR) had a significant negative correlation with R_{cwd} per sample ($r^{2=}0.21$, $p=0.002$, Figure 3.4). When FMR was correlated with the R_{cwd} values from each campaign, there was a positive linear correlation of the coefficients of determination (r^2 values) from each correlation and the non-log-transformed mean WSM from each campaign ($r^{2=}0.40$, $p=0.008$, Figure 3.5b).

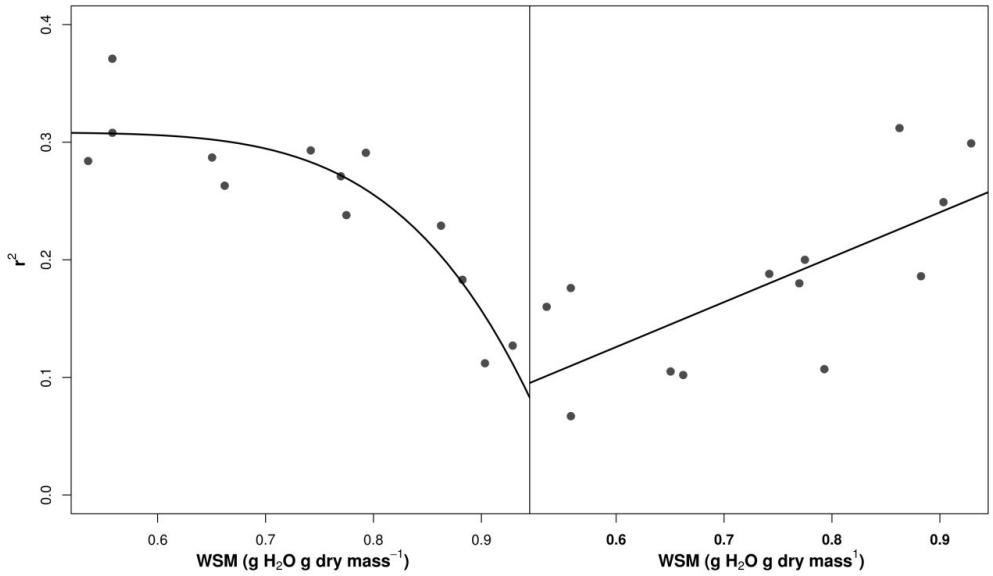

*Figure 3.5: Left panel: Asymptotic relation ((y=a+(b-a)*exp(-exp(c)/x), where a=0.308, b=-681.095, c=2.2044) with the mean woody surface moisture (WSM, g H_2O g dry mass^{-1}) values per measurement period,, and the r^2 values calculated from the linear relation between the log_{10} WSM and log_{10} R_{cwd} for each measurement period for all CWD samples. Right panel: Positive linear correlation with the mean WSM per measurement period and the r^2 values from the linear relation of the fractional mass remaining (FMR) and R_{cwd} for all CWD samples in each measurement period ($r^2=0.49$, $p=0.008$).*

3.4.4 Chemical analyses

The C:N ratio was 31.0 % lower in the external CWD samples (i.e. the xylem sampled closest to the bark, sapwood) than the internal CWD samples (samples from the centre of the CWD section, heartwood; Table 3.3), caused by 19.7 % higher N values and 3.1 % lower C values in the external CWD. Internal and external values of C, N, C:N ratio, lignin, cellulose, hemi-cellulose and ratios of lignin to cellulose and hemi-cellulose appeared to have little or no association with R_{cwd} .The only significant relationship was the log-transformed value of outer-xylem cellulose with R_{cwd} (r^2= 0.10 p=0.038). Linear correlations between fractional mass remaining (FMR) and wood chemistry suggested that there was no significant universal relation between previous decomposition of CWD and the woody tissue chemistry across the different species in this study.

	External (n=42)		**Internal (n=35)**	
	Mean	**SE**	**Mean**	**SE**
% C	38.6	1.95	39.8	1.95
% N	0.8	0.11	0.6	0.12
% Lignin	16.2	0.61	17.5	1.02
% Cellulose	32.6	1.75	34.3	2.12
%.Hemi-cellulose	6.2	0.33	5.4	0.36
C:N	121.2	16.36	158.8	22.57
Lignin: Celluose	0.54	0.03	0.58	0.05

Table 3.3 : Mean and standard error (SE) of CWD percentage content by mass of C, N, lignin, cellulose, hemicellulose are shown, and also the ratios of carbon to nitrogen and lignin to cellulose. External samples represented sapwood and were from the most external point of the radial section but underneath any bark. Internal samples represented heartwood and were taken from the closest point to the centre of the radial section.

3.4.5 Modelling CWD respiration sample variability

Stepwise regressions using all factors that showed a bivariate correlation with mean R_{cwd} per sample (WSM, WSG, FMR, and external cellulose content) revealed that a model including WSG, FMR and $\log_{10}$ WSM had the lowest AIC. WSG, however, was not a significant contributor to this model and an ANOVA indicated that a model including only FMR and mean WSM per sample was an equally good predictor of sample variability in $\log_{10} R_{cwd}$. A multiple linear model including these two factors explained 43.1 % of the sample variation in mean $\log_{10} R_{cwd}$ (R_{cwd} =0.084+(0.589*WSM)-(0.903*FMR)).

3.4.6 Modelling CWD respiration seasonal variability

The 13 estimates of R_{cwd} were scaled to the estimated biomass for a nearby plot (38.1 Mg ha^{-1}; see methods section). These scaled estimates, once log-transformed, also demonstrated a significant relationship with mean weekly SWC lagged by three weeks (r^2=0.48, p=0.009). We use this relationship, combined with the SWC data for 2011, to estimate daily changes in R_{cwd} for 2011. Over the period of our study, the range of SWC values which were recorded was between 0.11 and 0.22 $m^3 m^{-3}$; 76 % of the annual SWC values for 2011 were between the ranges of SWC recorded during our study period. As most of the total annual variability in the SWC for 2011 (0.11-0.26 $m^3 m^{-3}$) was captured by the measured range of SWC during our study period, we assume therefore that our relationship between R_{cwd} and SWC provides a good representation of the likely relationship over the whole of 2011.

The average of the standard errors on the 13 values of R_{cwd} shown in Figure 3.2 was 17.7 % of the mean values. Therefore a 17.7 % error was assigned to our extrapolated R_{cwd} data. Similarly we assume that these errors may be non-random due to potential bias from our scaling methods and therefore we sum daily errors to estimate the error on annual values of R_{cwd}. Results from this modelling process showed there was a strong seasonal pattern in R_{cwd} (Figure 3.6) and during the dry season there was a 20.5±5.1 % reduction in daily R_{cwd}. The sum of the daily predictions of R_{cwd} for 2011 was 1.66±0.29 Mg C ha yr^{-1}. Annual ecosystem respiration was 32.8 Mg C ha^{-1} yr^{-1}; therefore we estimate that R_{cwd} represents 5.1±0.9% of ecosystem respiration.

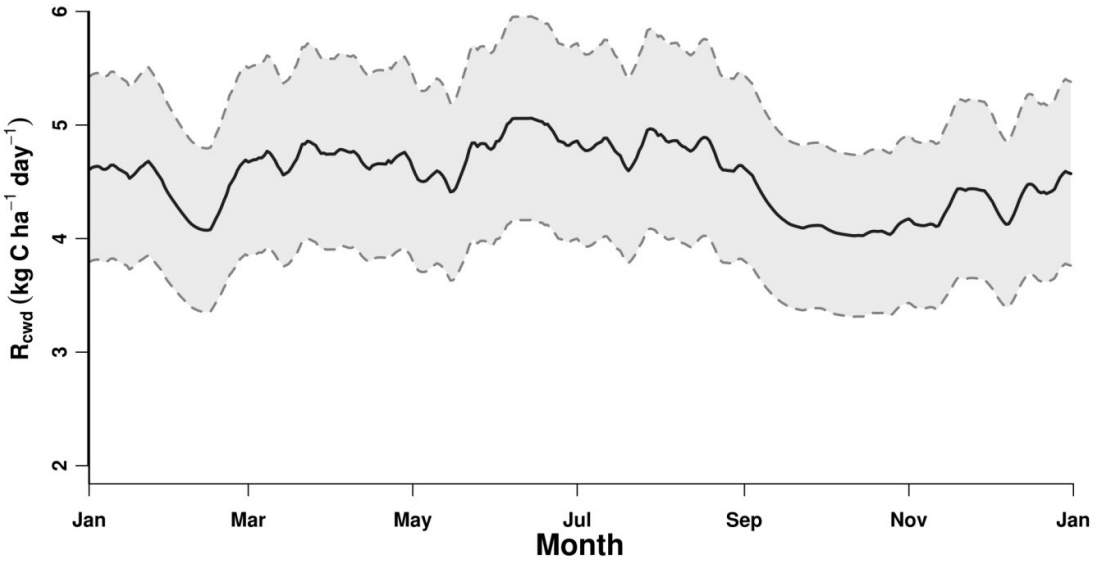

Figure 3.6: Modelled daily mean R_{cwd} (kg C ha^{-1} day^{-1}) for 2011 modelled from a relationship with average weekly SWC lagged by three weeks. Black line indicates the mean from a 6.25 ha forest inventory plot and grey dotted lines and shaded area indicate the standard error of the mean.

3.5 Discussion

3.5.1 Interaction of abiotic factors and CWD moisture content

This study demonstrates that reduced woody tissue moisture causes reductions in R_{cwd}, confirming hypothesis one. CWD moisture content is an important control over the variation of R_{cwd} in both tropical and temperate climates (Chambers et al., 2000; Chambers et al., 2001; Torres and Gonzalez, 2005; Jomura et al., 2007; Zhou et al., 2007; Forrester et al., 2012). Chambers et al (2001) hypothesised that drier CWD had lower R_{cwd} but responded positively and rapidly to increased moisture levels. As the CWD dried out over the dry season, the activity of fungal and bacterial decomposers would have declined, as the WSM reduced to low levels. This activity would then have increased rapidly following re-wetting. Consistent with this hypothesis and Chambers et al. (2001) we find that the drier CWD without contact with the ground has a strong response to seasonal changes in WSM, but this response is not significant in CWD samples with soil contact, which have WSM values which are 42.7±0.2 % wetter (Figure 3.3). The strength of the correlation between sample R_{cwd} rates and the mean woody moisture content of each sample changes between measurement periods, becoming stronger as the climate becomes drier and the mean WSM per campaign is reduced (Figure 3.5). As the dry season progresses moisture levels become more limiting for the activity of decomposers and therefore CWD moisture becomes a more important factor in controlling the variability of R_{cwd} between samples. If future climates over Amazonia are drier and the dry season becomes longer (Christensen et al, 2007; Harris et al., 2008; Li et al., 2008; Malhi et al., 2009a; Gloor et al., 2012), our results suggest that annual R_{cwd} rates will be reduced and that their responses to seasonal changes in soil and ambient air moisture

will be stronger and more tightly constrained.

In temperate forests temperature is the most important factor controlling decomposer activity, R_{cwd} and CWD decomposition rates (Jomura et al., 2007; Forrester et al., 2012). In contrast, here, we find that wood temperature is not related to seasonal changes in R_{cwd}. Almost all (97.3 %) of the wood surface temperature measurements taken across all campaigns had a narrow temperature range (24 and 30 °C), which was probably too small to yield a temperature signal in microbial respiration processes, given the natural variance in the data, and the dominance of the signal resulting from moisture constraints. The absence of a significant effect of temperature on respiration processes in tropical rainforests was also observed by Stahl et al. (2011) investigating living trunk respiration on the same forest plots and by Sotta et al. (2007) examining drought impacts on soil respiration, though we expect that had there been a sufficient change in temperature when moisture availability was not limiting, then a temperature response in R_{cwd} would have been observed.

VPD and SWC content both directly control the moisture status of the CWD and the humidity of the air inside the CWD. Consistent with this, SWC and VPD were very good predictors of seasonal change in R_{cwd} (Table 3.3.2), nevertheless a lag of three weeks had to be included in order to give the best prediction of R_{cwd}. This lag may reflect the time it takes for decomposers, such as fungi, to respond to changes in the moisture environment, or for moisture to fully penetrate the decomposing CWD tissue.

3.5.2 Seasonal variability of R_{cwd} and biotic scalar relationships

Alongside wood moisture content, a number of other factors are likely to influence how easily accessible CWD is to decomposers, and therefore how quickly it is decayed: wood density, wood decay status, diameter and chemistry (Chambers et al., 2000; Beets et al., 2008; Hérault et al., 2010; van Geffen et al., 2010). As R_{cwd} rates change according to some abiotic factors relating to moisture, we would expect relationships between biotic correlates which control the variability of R_{cwd} between samples to change across seasons, as observed in the relationship between WSM and R_{cwd} (Figure 3.5). We find that mean $\log_{10}$ R_{cwd} per sample has a strong relationship with WSG (Figure 3.4), but we find no seasonal pattern in the correlation of WSG to the sample R_{cwd} measurements from each period. FMR is a good indicator of the decay status of wood (Hérault et al. 2010) and we find it has a significant negative correlation with the mean R_{cwd} of each sample (Figure 3.4). FMR, like wood moisture content, is not a static scalar of R_{cwd} rates between samples. The strength of the relation is related directly to the mean wood moisture (Figure 3.5) and therefore the relationship between decay status and the R_{cwd} rate from different samples varies according to seasonal moisture conditions. We accept our second hypothesis that the strength of relationships of biotic variables with R_{cwd} changes with woody moisture values.

Wood chemistry influences the decomposition of the woody parts of angiosperm species because the chemical composition determines the proportion of decomposable material and its accessibility to decomposer communities (Weedon et al., 2009). However, we find only a weak relationship between R_{cwd} and the concentrations of cellulose in the external wood, and no relationships with C:N,

lignin, or hemi-cellulose. In agreement with other studies on wood decomposition, we find C:N ratios of tropical CWD are very low (Table 3.3) relative to CWD from other biomes (Clark et al., 2002; Torres and Gonzalez, 2005; van Geffen et al., 2010; Freschet et al., 2012); therefore N is likely to be less limiting on R_{cwd} and CWD decomposition in the tropics than in temperate regions. Due to the high energy and nutrient requirements for breaking down lignin (Weedon et al., 2009) we expected lignin concentrations to be negatively correlated with CWD respiration as found for decomposition studies in other tropical forests (van Geffen et al., 2010; Freschet et al., 2012), but we do not find lignin or the lignin:cellulose ratio to be a good correlate of $R_{cwd.}$ in this study. Correlations between CWD chemistry and decomposition remain unclear (Zhou et al., 2007), and other unmeasured wood chemical compounds, or the other controlling factors we have identified, appear to be more important determinants of R_{cwd} than the wood chemistry we examined.

3.5.3 Modelling R_{cwd} and predicting seasonal drought responses

Weekly mean SWC lagged by 3 weeks explained 48 % of the seasonal variation in mean $R_{cwd,}$ once it was scaled to a plot level using the mass of CWD on a nearby plot. SWC is a good indicator of seasonal drought severity and the moisture content of CWD, making it a good and easily-measured abiotic factor for modelling the seasonality of R_{cwd} as hypothesised (hypothesis 3). The results from this extrapolation show that in 2011 the annual sum of modelled daily R_{cwd} for the Paracou forest was 1.66±0.29 Mg C ha^{-1} yr^{-1}. This is equivalent to 5.1±0.9 % of the total ecosystem respiration in 2011, and therefore represents a significant flux of

ecosystem respiration as hypothesised (hypothesis 4). This estimate is close to the 6.4% estimated by Chambers et al (2004) at an old-growth forest near Manaus, Brazil, but lower than the ~19 % estimation by Huytra et al (2008) and a 15 % estimation by Palace et al (2008) at Tapajos, Brazil, a site with unusually high CWD stocks (resulting from recent high mortality) at the time of measurement (Rice et al., 2004).

Our mean annual R_{cwd} estimate is slightly lower than the range of R_{cwd} estimated for other tropical rain forests (1.9-5.7 Mg C ha yr^{-1}, Chambers et al., 2001; Chambers et al., 2004; Huytra et al., 2008; Palace et al., 2008; Rice et al., 2004). Although these data on R_{cwd} remain sparse, this slight discrepancy with published values may result from calculating CWD from census data which accounts for CWD from dead trees but not for other sources such as fallen branches; CWD estimation from census data has been found to underestimate the volume of CWD by 30-50 % (Palace et al., 2008). If we increase our R_{cwd} estimate by 30 %, the lower estimate from Palace et al. (2008), R_{cwd} would reach 2.16±0.38 Mg C ha^{-1} yr^{1}, 6.6±1.2 % of R_{eco}, and well within the range of estimates from the other tropical forest studies.

R_{cwd} from this forest is reduced by 20.5±5.1 % during the dry season (Figure 3.6). This is consistent with other studies which have shown that moisture availability is a principal limiting factor on respiratory processes in tropical ecosystems (Goulden et al., 2004; Sotta et al., 2007; Bonal et al., 2008; Meir et al., 2008; Metcalfe et al., 2010; Stahl et al., 2011). The extent of the seasonality we observe in R_{cwd} is slightly lower than the fractional reduction in R_{eco} and soil respiration on these plots from wet to dry season (~30%, Bonal et al., 2008) and the reduction in live woody tissue

respiration from stems of (31%; Stahl et al., 2011). Thus, short-term (seasonal) reduction in soil moisture appears to cause a coherent reduction across most of the respiration pools in this forest, though the fractional decline varies among components. The contribution of R_{cwd} to R_{eco} and NEE will therefore vary throughout the year, making it important to understand and model seasonal changes in this and other respiration fluxes (Meir et al., 2008).

3.5.4 Uncertainties with modelling R_{cwd}

It is possible that there is some bias in our plot-scaled R_{cwd} estimates, because of assumptions made in the scaling process. First, we assume that the 33 samples which were used to estimate the mean respiration rate were representative of the mean respiration rate of this forest. We found R_{cwd} to vary by over 2 orders of magnitude between CWD samples (as also found by Chambers et al. (2001)), and therefore suggest that the true forest mean R_{cwd} rate is likely to be captured in the error around the mean of our 33 samples. However this assumption cannot be tested without substantial further sampling.

Secondly, we model current CWD biomass using forest census data which has been shown to under-estimate biomass (Palace et al., 2008). We therefore suggest that our total forest R_{cwd} error could be a substantial underestimation. However, large scale CWD biomass studies, which themselves are associated with substantial uncertainty (Chao et al., 2009), would be required to estimate this uncertainty, and this was beyond the scope of this study.

Lastly, seasonal variation in SWC only explained 48 % of the variation in R_{cwd} once scaled to a plot level and therefore a substantial amount of variation was caused by other factors. Assessing the effect of the decomposer community on R_{cwd} was beyond the scope of this study. However, the volume and type of decomposer in CWD will have substantial effects on the between-sample variation in R_{cwd} (Harmon et al., 1986; Förster et al., 2006; Cornwell et al., 2009; Palin et al., 2011; Freschet et al., 2012). Termites are considered one of the few decomposers that have a significant impact on Amazon wood decomposition (Palin et al., 2011). They are responsible for 20 % of CWD decomposition in some Amazon forests and have been estimated to release directly up to 1.9 Pg C yr^{-1} to the atmosphere from tropical regions (Cornwell et al., 2009). Out of the 42 CWD woody tissue samples in this study, 31 showed evidence of termite attack, and we observed that the numbers of termites visible on the samples could change quite dramatically between measurements, which we suggest may alter R_{cwd} (Appendix 1). There was significant noise in the seasonal R_{cwd} data in CWD samples where high visual evidence of termites was also noted. We found termites were more common and abundant in the CWD in contact with the soil, and this may be a factor which contributes to the lack of a significant seasonal response to wood moisture content in these samples (Figure 3.3). However, despite any variability in R_{cwd} contributed by the presence and activity of termites in some of our samples, we still observed a significant relationship between the mean R_{cwd} rates and physical factors which are indicative of seasonal drought (Table 3.3.2).

3.6 Conclusions:

This study shows that R_{cwd} in a tropical rainforest submitted to strong seasonal variations in climatic conditions is not a constant flux but is very sensitive to seasonal variations in water availability, which, in this forest, causes a reduction of approximately 20 % in R_{cwd} from wet to dry season. Reductions in the amount of respired carbon from the CWD pool are controlled by reductions in wood moisture content, which restrict the activity of decomposer communities. Seasonal reductions in R_{cwd} were substantial in CWD samples which had lower initial wood moisture contents, and therefore suffered more severe restrictions in water availability throughout the dry season.

We find that changes in SWC content are a good predictor of seasonal changes in mean R_{cwd}. In contrast with other biomes, as the range in temperature variation tends to be small in this environment, temperature is clearly not the main constraint on R_{cwd} in tropical rainforest; any temperature signal there might have been in our data was dominated by the water constraint. Any future increases in drought severity or length are likely to cause substantial reductions and greater seasonal difference in R_{cwd}. We estimate that R_{cwd} is ~5 % of annual $R_{eco,}$ however if mortality rates were to increase, for example through increased drought severity (Marengo et al., 2009, Phillips et al., 2009, da Costa et al., 2010, Lewis et al., 2009) changes in R_{cwd} are likely to become increasingly important in controlling NEE and seasonal variations in R_{eco}. Our results suggest that to predict accurately the future carbon balance of Amazonian forest, land surface models need to include both a CWD pool and a moisture-response function determining respiration processes in CWD.

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Chapter 4: Quantifying the effects of seasonal drying on the carbon storage and carbon use efficiency of an Amazonian forest.

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4.1 Abstract

The carbon balance of tropical forests is an important regulator of atmospheric carbon dioxide (CO_2), yet the state of these forests as a source or sink of CO_2 remains uncertain. We combine the information from an ecosystem carbon cycle model with nine ecological data time series from a forest in eastern Amazonia. The observations include respiration from wood, foliage, coarse woody debris and soil, as well as leaf area index, woody biomass, litter-fall, wood diameter growth and net ecosystem exchange. All observations were measured in both the wet and dry season. This study is the first to combine the information provided by both model and measurements to quantify, with estimates of uncertainty, the seasonal changes in the carbon balance of a tropical forest site which experiences a pronounced dry season. We find that this forest stores 341±36 g C m^{-2} yr^{-1}; however the daily carbon storage was four times greater in the dry season than in the wet season. The data assimilation (DA) analysis showed that the increased dry season carbon storage was caused to an equal extent by a decrease in ecosystem respiration and an increase in gross primary productivity (GPP). We found that reductions in heterotrophic respiration in the dry season, in response to decreased soil water availability was greater than the reduction in ecosystem respiration and compensated for a small increase in autotrophic respiration in the dry season. The average carbon use efficiency (CUE) of this forest was 0.36±0.2. A greater increase of GPP than autotrophic respiration in the dry season caused a 5.38±0.3 % increase in dry season CUE. This small change suggests that this forest maintains a similar efficiency at investing carbon into biomass between wet and dry season. We therefore conclude that changes in the net carbon storage of this forest are mostly driven by a decrease in heterotrophic respiration in

response to reductions in the soil water content and by dry season increases in GPP.

4.2 Introduction

Amazonian rainforests are a significant global store of carbon with very high rates of carbon cycling. These forests have the potential to be a large source or sink of atmospheric carbon (Gloor et al., 2012). Therefore, understanding how these forests respond to changes in climate is of great importance**.** Elevated concentrations of atmospheric CO_2 and increasing temperature have been predicted to cause longer and more intense dry seasons in the Amazon, as well as reductions in wet season rainfall (Betts et al., 2004; Cox et al., 2004; Huntingford et al., 2004; Li et al., 2006; Jupp et al., 2010). Extreme seasonal events, such as the 2005 and 2010 Amazon droughts, are also predicted to occur more frequently (Cox et al., 2008; Marengo et al., 2008; Marengo et al., 2011). We need therefore to better understand the response of Amazonian forests and their carbon balances to seasonal changes in climate.

The seasonality of the carbon balance of Amazon forest remains uncertain. Existing studies in the Amazon forest have reported both increases (Saleska et al., 2003; da Rocha et al., 2004; Goulden et al., 2004; Hutyra et al., 2007; Bonal et al., 2008) and decreases (Malhi et al., 1998; Chambers et al., 2004; Keller et al., 2004) in the total carbon stored in tropical forests in the dry season. Models struggle to adequately simulate these seasonal changes (Saleska et al., 2003; Baker et al., 2008; Verbeeck et al., 2011). The relative importance of seasonal changes in gross primary production (GPP) and components of ecosystem respiration (R_{eco}) remains unresolved.

Recent model development has focused on adapting seasonal patterns of root water uptake and phenology to improve simulation of seasonal patterns of tropical forest fluxes (Lee et al., 2005; Baker et al., 2008; Grant et al., 2009; Kim et al., 2012).

However, such studies have focused on improving the simulation of gross primary productivity (GPP) and have given little attention to improve the simulation of the fate of fixed carbon, including the components of ecosystem respiration. Ecosystem respiration is made up of multiple autotrophic (leaf, root and stem) and heterotrophic (litter, dead wood and soil) components. Various carbon budgeting papers have estimated the contribution of each component of respiration to total R_{eco} (Malhi et al., 2009; Metcalfe et al., 2010; Malhi et al., 2013). However, there is still significant uncertainty regarding how sensitive components of R_{eco} are to seasonal drying and how this sensitivity affects seasonal changes in the carbon budget.

The response of ecosystem respiration (R_{eco}) in tropical forests remains poorly understood compared to photosynthesis (Meir et al., 2008). Carbon use efficiency (CUE; the proportion of GPP which is invested into net primary production, with the remainder expended as autotrophic respiration), is an important determinant of respiration (Waring et al., 1998). CUE is difficult to quantify accurately using measurements because of uncertainty associated with scaling multiple measurements of leaf, stem, and root respiration to an ecosystem scale. Similarly estimating CUE remains a challenge for models in tropical systems, because of uncertainties in parameterising seasonal changes in autotrophic respiration (R_{auto}) in models (Fox et al., 2009; Verbeeck et al., 2011).

In this study an established data-assimilation technique (Knorr and Kattge, 2005; Richardson et al., 2010; Hill et al., 2012), is used to combine observations with a mass balance model. The outcome is an analysis of how seasonal drying at a tropical forest site alters the carbon balance of the ecosystem, consistent with observational

and model uncertainty. This approach provides an opportunity to comprehensively assess the seasonal changes in the carbon budget of this ecosystem. It is the first model-data fusion study which has the capability to directly attribute, with estimates of uncertainty, the seasonal changes in the carbon balance to changes in the component carbon fluxes of a tropical forest.

The study is performed for a lowland tropical forest at the Paracou research station in French Guiana, where multiple ecological data sets are available. Initial studies indicated a change of approximately 10 % in photosynthetic activity between the dry and wet season (Bonal et al., 2008), which is low compared to respiration fluxes (Bonal et al., 2008; Stahl et al., 2011; Rowland et al., in review). Consequently the seasonal change in the carbon balance of this forest would appear to be very dependent on seasonal changes in respiratory fluxes. The site experiences a strong seasonal change in soil moisture availability (Bonal et al., 2008; Wagner et al., 2011), which is linked to reductions in soil respiration (including root and litter respiration), stem respiration and coarse woody debris (CWD) respiration (Bonal et al., 2008; Stahl et al., 2011; Wagner et al., 2012; Rowland et al., in review). We use the data available from this site in a data assimilation set up with a detailed photosynthesis model, SPA (Williams, 1996; Fisher et al., 2007) and a simple carbon box model (DALEC-fg, Williams et al., 2005) to address the following questions and hypotheses:

- Q1: How does the carbon allocation and respiration from the leaves, stems and roots vary between wet and dry season?

  H1a: There will be no change in allocation across seasons.

H1b: The respiration of carbon from the leaves, stem and roots will show little seasonal variation.

- Q2: Do changes in gross primary production, heterotrophic respiration or autotrophic respiration have a greater influence on seasonal changes in the carbon balance?

  H2a: Dry season reductions in heterotrophic respiration will cause the greatest change in the carbon balance of this forest.

  H2b: Autotrophic respiration will be the largest source of respiration in both wet and dry season.

- Q3: Does the carbon use efficiency of this forest vary between wet and dry season?

  H3: There are no significant changes in carbon use efficiency because seasonal changes in autotrophic respiration and gross primary productivity are small.

4.3 Methodology

4.3.1 Site

The study focused on a tropical lowland forest site at Paracou Research Station in French Guiana (5°16 N, 52°16 W). Data were collected over a period of 8 years from January 2004 to December 2011 on two adjacent 70 x 70 m *terra firme* permanent forest plots. The plots were situated on nutrient-poor acrisols and were similar in ecological characteristics, including species density (103 and 116 species per ha),

stem density (612 and 725 stems per ha), and litter-fall (7.28±0.3 and 6.42±0 .3 Mg ha^{-1} yr^{-1}). French Guiana has a strong seasonal rainfall pattern caused by the movement of the inter-tropical convergence zone twice a year, causing a long (August-November) and short (March) dry season. Consequently, despite the site receiving an average of 3,041 mm of rain per year (Gourlet-Fleury et al., 2004), during the long dry season rainfall is normally <50 mm per month (Bonal et al., 2008).

4.3.2 Model Description

4.3.2.1 Overview

The carbon cycle model used in this study in French Guiana was an adapted version of the Data Assimilation Linked Carbon Model (DALEC; Williams et al., 2005; Fox et al., 2009) described in Figure 4.1 and Table 4.1 (hereafter referred to as DALEC-fg). DALEC-fg is a simple box carbon cycle model of carbon pools connected by fluxes. Alterations to DALEC included: 1) inclusion of a coarse root pool and a coarse dead wood (CWD) pool; 2) Respiration from foliage, wood, coarse roots and fine roots are predicted as a fraction of the allocation to each of these pools; 3) A moisture and a temperature response function (described below) were used to predicted heterotrophic respiration; 4) Separate parameters for dry and wet season allocation, turnover rate and respiration from the foliage, stem and root carbon pools were used.

DALEC-fg's computational simplicity and ability to run on a daily time-step makes

it well suited to DA where large model ensembles are required. GPP in DALEC-fg was determined using the Aggregated Canopy Model (ACM, Williams et al., (1997) Figure 4.1). ACM is an empirical simplification of the Soil–Plant–Atmosphere model (SPA; Williams, 1996) which predicts GPP according to daily minimum and maximum temperature, precipitation, radiation, atmospheric CO_2 concentration, soil water potential, hydraulic resistance, leaf nitrogen and leaf area index (LAI) combined with 10 optimised parameters. To ensure ACM was correctly calibrated for the study site, we optimised the 10 parameters in ACM to reproduce the GPP predicted by a set of runs from the SPA model. SPA was run on a half hourly time-step for our study area over the period 2004-2011. SPA has previously reproduced realistic GPP values for sites in the Amazon (Fisher et al., 2007), calibrated from detailed leaf level measurements (Fisher et al., 2006). We calibrated SPA using detailed leaf data recorded at the site in 2011 (Bloomfield, 2012; Zaragoza-Castells et al., in prep) which suggested V_{cmax} was 52.4±1.9 μ mol m^{-2} s^{-1}, J_{max} 63.7±2.2 μ mol m^{-2} s^{-1}, LMA was 122.1±2.2 g m^{-2}, and leaf nitrogen content was 1.9±0.1 g m^{-2} . In addition we set minimum leaf water potential to -2.5 MPa in SPA. The clay and sand contents used to calibrate the soils in SPA were taken from data collected at the site and published in Epron et al. (2006). An optimisation routine (optim function, R-project software, http://www.r-project.org R 2.14.2) which minimised the difference between ACM's predicted GPP and the daily GPP estimated by SPA was used to calibrate the 10 parameters for ACM. To ensure the optimisation was not biased to a specific LAI, SPA was run with a range of LAIs from 3–10 m^2 m^{-2}

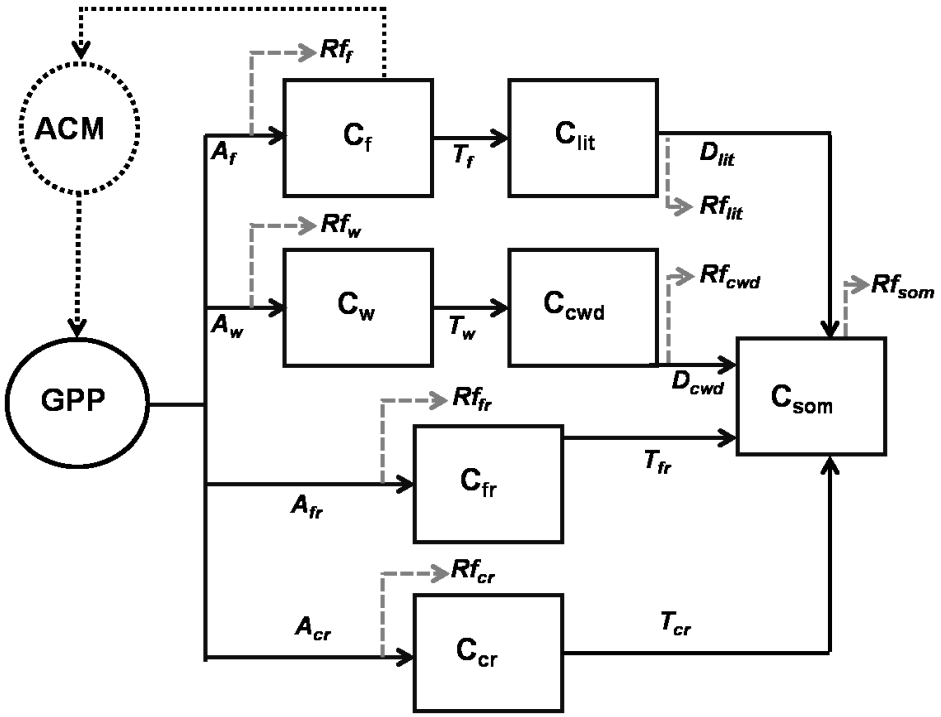

Figure 4.1: Diagram of the DALEC-fg carbon model. The boxes represent a carbon pool and the arrows represent a carbon flux through the model, the dotted grey arrows represent a loss from respiration. All of the acronyms for the pool and fluxes are explained in the model parameters table (Table 1). The fractions respired from autotrophic pools (foliar carbon; $C_{f,}$ carbon in wood; $C_{w,}$ carbon in fine roots; $C_{fr,}$ and carbon in coarse roots C_{cr}) are calculated as a fraction of the carbon allocated to the pool. The fraction respired from the heterotrophic pools ($C_{lit,}$ $C_{cwd,}$ C_{som}) are calculated as a fraction of the total pool.

4.3.2.2 *Soil Moisture response function in DALEC-fg*

The soil moisture response function was calculated using the measured mean daily soil respiration (R_s). The R_s data included respiration from root, litter and soil organic matter. To remove the effect of root respiration and only account for changes in heterotrophic respiration firstly we assume that root respiration does not vary from

wet to dry season and that all of the seasonal changes in soil respiration are caused by heterotrophic processes. Previous studies in the eastern Amazon have found that heterotrophic soil respiration response to reductions in soil moisture is strong (Metcalfe et al., 2007; Sotta et al., 2007). In comparison only very small changes in autotrophic soil respiration have been found (da Costa et al., in press), and in some cases small increases in dry season root respiration rates have been found (Metcalfe et al., 2007). Secondly we assume root respiration is approximately half of the mean annual soil respiration as has been found at our study site (Ponton; unpublished data) and at other sites in the eastern Amazon (Metcalfe et al., 2007; Metcalfe et al., 2010). Using these assumptions we estimate daily root respiration to be a constant value of 1.9±0.3 g C m^2 d^{-1}, (half of the mean soil respiration efflux) and subtract this value from all daily R_s data (n=601, 2005-2006) to estimate heterotrophic soil respiration.

Before creating a response function between heterotrophic soil respiration and soil water content (SWC) the seasonal effect of temperature on the heterotrophic respiration from soil was removed by subtracting the change in heterotrophic respiration caused by temperature using the temperature response function in DALEC-fg, which assumes a doubling of respiration rate with a 10°C rise in temperature. The remaining seasonality in the heterotrophic soil respiration was regressed against the mean measured daily surface soil water content (described below) and a log normal curve fitted to this data (Figure 4.2). We tried using the quadratic curve used by Sotta et al., (2004) and Sotta et al., (2007) to fit soil water content to soil respiration in the tropics, however, this produced non-random distributions of the residuals introducing biases in the relationship. We normalised the log normal curve in Figure 4.2 so the optimum point was 1. We provided

DALEC-fg with the measured SWC data and used the normalised log normal function to adjust predicted values of carbon loss from the heterotrophic pools based on soil moisture. It should be noted that this moisture response function is an empirical relationship that is site specific.

4.3.2.3 *Defining wet and dry season*

Dry season was defined using the soil water content values, as all days where the mean daily SWC was below a threshold of 0.124 m^3 m^{-3}. This threshold was set as the lower quartile of all the SWC data which had a mean and standard deviation of 0.17±0.04 m^3 m^{-3}. This threshold ensured that the dry season was maintained as days during the annual long dry season. In total 733 out of 2922 days were defined as dry season. The wet-dry season division was used to define when the model could switch between wet and dry season parameters for the allocation, residence time and respiration parameters for the autotrophic carbon pools (foliar carbon (C_f), carbon in wood (C_w), and carbon in fine and coarse roots (C_{fr}, C_{cr}). The seasonal changes in these parameters were used to allow the data assimilation analysis to adjust for variation of these parameters which may be required to enable the model to replicate the observed patterns in the data.

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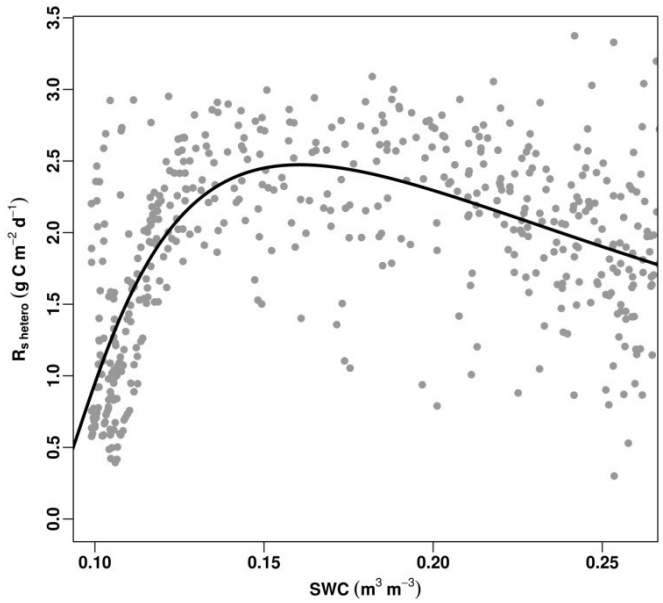

Figure 4.2: Relationship between daily average soil water content (SWC m^3 m^{-3}) from surface 10cm and heterotrophic soil respiration (R_{s_hetero}). R_{s_hetero} (shown in grey points) is derived from the measured daily average soil respiration (g C m^{-2} d^{-1}) corrected to remove the effects of temperature response and respiration from roots. A log normal curve is fitted through these points (black line; y= c(1/((swc+d)*sqrt(2pi.a^2)))* exp -((log(swc+d)-b)^2/(2 a^2))), where a=1.04, b=-1.45, c=0.088 and d=-0.08.*

4.3.3 Data Assimilation Methodology

The data assimilation scheme optimized 36 parameters, separate parameters for the wet and dry season allocation and turnover rate and respiration parameters for the autotrophic pools was included in these 36 parameters (Table 4.1). A DA scheme was set up using a Metropolis-Hastings DA scheme (Knorr and Kattge, 2005). This data assimilation technique generates a 'best-guess', *posterior*, distribution of model parameters. Many combinations of parameters are tried using a method that builds on success, defined as minimising an objective function which describes the difference

between assimilated data and model simulation. Parameter 'guesses' are constrained using another objective function which punishes parameter guesses which go outside of estimated prior ranges. Model parameters were assumed to be real, positive and to have a lognormal probability distribution (Knorr and Kattge, 2005). Therefore all processes of 'parameter guessing' and acceptance and rejection of parameters in relation to prior ranges were performed in log-normal space (see Knorr and Kattge. (2005) for details). The acceptance and rejection of proposed parameters based on model data comparisons was done in real space.

The step size for the 'parameters guesses' in the data assimilation was set to a random draw from a normal distribution, with a mean of 0 and a standard deviation of 0.004 in log normal space. Typically 40–45 % of proposed parameter steps were accepted with this data-assimilation (DA) scheme. The length of the Markov chain was determined by using Gelman-Ruben convergence statistic (Brooks and Gelman, 1998). The Gelman-Ruben convergence statistic was calculated using six Markov chains and indicated that after 1,200,000 steps the Markov chain had adequately sampled the posterior distribution, with a convergence levels below the 1.2 threshold suggested by Brooks and Gelman (1998). A burn point – the number of initial accepted parameter combinations which are thrown away – was set at 200,000 to ensure that we did not sample the initial portion of the chain, whilst parameters diverged from their initial values. Our final posterior distributions for each separate Markov chain was therefore made up of 1,000,000 accepted parameter combinations. The mean and standard deviations on the parameter combinations were calculated from the accepted parameter combinations.

4.3.4 Assimilated Data

4.3.4.1 NEE Data

Eddy covariance data on a half hourly time-step from 2004–2011 were available from a tower located < 50m from our study sites. The detailed methodology for the set-up of the tower has been described by Bonal et al., (2008). The NEE data was processed using ALTEDDY and standard quality control checks were used to filter the data (Foken et al., 2005). Following Bonal et al., (2008) all night-time NEE data for which U* values were <0.15 m s^{-1} were filtered out. As some spurious spikes were still visible in the half hourly carbon flux (FC) and carbon storage data (SFC) we filtered all values of SFC and FC greater than 10 standard deviations from the mean (in both cases <0.11 % of the data were filtered). To create daily values of NEE, only days with ≥40 half hours per day were used. Missing values for these days were replaced with the mean daytime or night-time value for that day, before fluxes were summed. From 2004-2011, 497 daily values of NEE were available. Estimates of error on NEE data were necessary to determine the confidence in the data estimation. The DA uses data errors when determining how close model simulations are to data. NEE error estimates were generated on a half hourly time-using the method described in Hollinger and Richardson (2005). The error estimates were divided into 12 categories based on month of the year to account for seasonal changes in the error. When plotted, the errors for each month formed a double Laplacian distribution, from which 48 points were randomly sampled and added to produce a daily error estimate (Hill et al., 2012). This sampling was repeated 50,000 times on error estimated from each month and the standard deviation of the samples

was used as the estimation of the error on the NEE values for the daily separated by month.

4.3.4.2 *Foliar data*

Leaf respiration measurements were available on our study plots from Stahl et al. (in press) for November 2007, July 2008 and November 2008, and from Zaragoza-Castells et al. (in prep) for the dry season of 2010. The data included the average and standard deviation of leaf respiration in dark conditions from fully sunlit leaves and which were adjusted to the mean daily temperature over our study period (25.6 °C). We estimated the fraction of sunlit and shaded leaf area using the same method as Malhi et al., (2013), which suggested 1.69 m^2 m^{-2} of the LAI was sunlit and 4.6 m^2 m^{-2} was shaded. To account for lower respiration in lower canopy leaves we used estimates from Domingues et al., (2007) at the Tapajos forest, Brazil, which showed that respiration in the mid canopy was ~43 % of the values of the fully sunlit upper canopy. The inhibition of leaf respiration during the daytime (Atkin et al., 2000; Atkin and Macherel, 2009) was accounted for by assuming that leaf respiration during daytime hours (12 hours per day) was inhibited by 33 % of compared to respiration which occurred at night through using the equation reported in Atkin et al., (2000). This method has been previously applied in other papers modelling carbon exchange in tropical forests (Malhi et al., 2009; Malhi et al., 2013). The error on the leaf respiration data was calculated through propagating errors from leaf level respiration, and LAI measurements.

Mean LAI and standard deviation was estimated from measurements made with the

LICOR LAI 2000 at between 37 and 49 points per plot in March 2005, November 2005, November 2008, September 2010, March 2011 and September 2011. LAI was compared to model output using an estimate of leaf mass per area (LMA) of 122.07±2.23 g C m^{-2}, measured at the site on 70 leaves by Zaragoza-Castells et al., (in prep). LMA was given as a parameter to the ACM model to allow it to convert foliar carbon to LAI.

On our study sites litter-fall was measured monthly from January 2004 to December 2011 using four 1 m^2 litter traps on each plot (n = 8). Material was collected, dried to a constant mass and then weighed.

4.3.4.3 *Woody stem data*

Respiration from stems was measured on our study plots by Stahl et al., (2011); stem respiration measurements were made over 11 periods, during both wet and dry season, between September 2007 and February 2009. The mean and standard error of these measurements were scaled to plot level using surface area of the stems per unit of ground area (stem area index (SAI); (Chambers et al., 2004; Robertson et al., 2010). SAI accounts for the area of large branches and a detailed description of the calculation of SAI can be found in Chambers et al., (2004). The error on stem respiration was derived from the measurement error following scaling and therefore we assume that the scaling error was captured by the measurement error.

A census of the diameters of all trees ≥ 10 cm diameter at breast height (DBH, 1.3m) was conducted in 2004, 2006, 2008 and 2010. We used these measurements to estimate the total biomass of the plots between using the biomass equation for

tropical moist forests from Chave et al., (2005), which included tree height; tree height was calculated from diameter using a country specific equation in Feldpausch et al. (2011). As no error estimation existed for biomass we set the standard error to be 10 % of the value.

Tree diameter increment data from Wagner et al., (2012) were measured 32 times for 114 trees on a monthly to bi-monthly basis from 2007-2010 on our study plots. Tree diameter measurements were converted to tree biomass using the same method used for wood biomass. To avoid scaling errors we did not directly assimilate the tree biomass increment for the following reasons: Firstly, the 114 trees measured were not representative of the structure of the 674 trees on the two plots (Wagner et al., 2012). Secondly, the carbon used for diameter growth is not the same as the net carbon allocated to the stem, because carbon will be used for other processes within the stem. Instead we use the biomass growth data from these 114 trees to calculate the ratio of dry to wet season (defined below) biomass accumulation. Using the mean of 11 dry season and 21 wet season measurements from all 114 trees we calculated that the ratio of dry to wet season biomass accumulation was 0.40±0.09. This data was assimilated annually to provide the model with information of the approximate magnitude and direction of the seasonal change in woody biomass allocation.

4.3.4.4 *Heterotrophic respiration data*

R_{cwd} was estimated from 429 measurements made on 33 samples during 13 periods from July 2011 to November 2011, and reported in Rowland et al. (in review). We use the R_{cwd} estimates for the 13 measurement periods from Rowland et al. (in

review) scaled to the mass of coarse woody debris (CWD) on a 6.25 permanent forest plot <100m from our sample plots; full details of measurements and scaling methods for the R_{cwd} measurements are available in Rowland et al. (in review).

Soil respiration (R_s) data at the study site were measured by one of us (SP; unpublished data) from April 2005 to December 2006. R_s were measured every half hour on the study site using four automated chambers (a detailed discussion of equipment and methods used are available in Bonal et al., 2008). The chambers were placed on top of the surface litter and were then averaged into daily values. Respiration measurements therefore represent the combined respiration from surface litter, root litter, roots and soil. Error was derived from the standard error on the four chamber measurements. Data was however, only used when 3 or more of the soil chambers recorded measurements (577 days). There was significant autocorrelation in the R_s data which was removed by filtering the data to every 30 days (n=19). To maintain consistency with the assumptions made in the soil moisture response we assimilate R_s data separated into autotrophic and heterotrophic components as detailed above.

4.3.4.5 *Steady state observations and error estimation*

The model in its standard form makes no assumption of steady state, however because these are old growth forests they are likely to be close to steady state. Therefore, to ensure that the modelled carbon pools were close to steady state, we assimilated seven additional pseudo observations which were the change in size of each of the seven carbon pools in the DALEC-fg model. These observations had a

value of 0 and a standard deviation of 2 % of the size of the pool. This solution was necessary because computational limits prevented running the model until it was in steady state, as part of the assimilation process.

Standard error was used as an estimate of uncertainty on the assimilated data (Richardson et al., 2010). When combining errors (e.g. for example multiplying leaf respiration by LAI), the errors were assumed to be random and uncorrelated.

4.3.5 Prior information

Where possible priors on states and parameters were estimated using data from published and unpublished data from the study site. Where site data were not available estimates from studies on nearby sites in northern Brazil were used. Where no data existed the parameters were set to a best approximation or to the default values for DALEC-fg, with a higher error. All the prior values were assigned set a standard deviation of 0.25, 0.5 or 0.75 in log normal space (Knorr and Kattge, 2005; Table 1). These values were assigned based on an assessment of the uncertainty of the data source and on creating realistic limits on the mean estimate.

4.3.6 Soil Water Content Data

Soil water content (SWC) data was taken every 30 minutes from two probes at the study sites. For 2004-2008 data was available from a frequency domain sensor (CS615; Campbell Scientific Inc.) at 0.05 m depth 15m from the flux tower. Data

was available from a second frequency domain sensor (CS616; Campbell Scientific Inc.) inserted at 0.10 m depth, 10 meters from the flux tower for 2007-2011. To get continuous soil water content data series we used data for 2007-2011 from the CS616 probe averaged into daily mean values combined with mean daily SWC values from the CS615 probe for 2004-2006, corrected for the effects of differences in probes and depth. Daily mean SWC values from the CS615 were depth adjusted using an empirical regression between the mean daily values of SWC from the two probes during 2007 (r^2=0.82, $p<0.001$). Three were 72 gaps in the daily 2004-2011 SWC dataset; mean gap length was 8±9 days. These gaps were filled, where possible, with corrected data from the CS615 probe (n=52), otherwise the gaps were filled using the average of the 3 data points either side of the gap (n=20).

Table 4.1: Parameter descriptions for the DALEC-fg model, including their symbols (s), units, prior value (P), prior lower estimate (PL) and prior upper estimate (PU), the posterior median (Pos), the 15.9th (PosL) and 84.1th (PosU) quantiles on the posterior parameter distributions, and sources of the priors estimates for the DALEC-fg model. For allocation, turnover rate and respiration parameters for the autotrophic pools the wet season posterior parameter values are shown followed by the dry season posterior parameter values in brackets.

Parameter	**S**	**Units**	**P**	**PL**	**PU**	**Pos**	**PosL**	**PosU**	**Source of prior**
Initial foliage C stock	C_f	g C m^{-2}	384	299	493	421	411	431	Estimated from LMA data & LAI data
Initial wood C stock	C_w	g C m^{-2}	23553	18343	30243	22093	21015	23186	See methods section
Initial fine root C stock	C_{fr}	g C m^{-2}	371	289	476	469	373	568	Galbraith (2010)
Initial coarse root C stock	C_{cr}	g C m^{-2}	1593	966	2627	2970	1814	4610	Galbraith (2010)
Initial litter C stock	C_{lit}	g C m^{-2}	300	182	495	358	264	474	Malhi et al. (2009)*
Initial coarse wood debris C stock	C_{cwd}	g C m^{-2}	1738	1354	2232	1948	1550	2649	See methods section
Initial soil organic matter C stock	C_{som}	g C m^{-2}	29000	22585	37237	36820	30368	45195	Epron et al. (2006)
Allocation fraction to foliage	A_f	Fraction	0.43	0.26	0.71	0.40 (0.31)	0.38 (0.30)	0.42 (0.33)	Malhi et al. (2009)*
Allocation fraction to wood	A_w	Fraction	0.26	0.16	0.43	0.24 (0.18)	0.22 (0.17)	0.26 (0.18)	Malhi et al. (2009)*
Allocation fraction to fine roots	A_{fr}	Fraction	0.23	0.14	0.37	0.29 (0.45)	0.25 (0.41)	0.33 (0.47)	Malhi et al. (2009)*
Allocation fraction to coarse roots	A_{cr}	Fraction	0.08	0.05	0.13	0.06 (0.06)	0.04 (0.04)	0.10 (0.09)	Malhi et al. (2009)*
Turnover rate of foliage	T_f	Fraction of pool d^{-1}	2.4e-3	1.8e-3	3.0e-3	1.7e-3 (2.1e-3)	1.6e-3 (2.0e-3)	1.7e-3 (2.2e-3)	Estimated from LMA and litter-fall (see methods).
Turnover rate of wood	T_w	Fraction of pool d^{-1}	2.5e-5	1.9e-5	3.2e-5	2.2e-5 (2.4e-5)	1.8e-5 (1.9e-05)	2.6e-5 (3.1e-05)	Rutishauser et al.(2010)

Turnover rate of fine roots	T_{fr}	Fraction of pool d^{-1}	1.4e-3	6.5e-4	2.9e-3	4.5e-3 (1.5e-3)	3.5e-3 (9.1e-3)	5.7e-3 (2,2e-5)	Trumbore et al. (2006)
Turnover rate of coarse roots	T_{cr}	Fraction of pool d^{-1}	2.5e-5	1.5e-5	4.1e-5	3.8e-5 (2.8e-05)	2.1e-5 (1.8e-5)	6.4e-5 (4.5e-5)	Assumed to be the same as T_w
Turnover rate of litter	D_{lit}	Fraction of pool d^{-1}	1.0e-3	4.7e-4	2.1e-3	1.1e-3	6.7e-4	2.0e-3	Metcalfe et al. (2010)
Turnover rate of CWD	D_{cwd}	Fraction of pool d^{-1}	4.4e-5	2.1e-5	9.3e-5	8.6e-5	4.9e-5	1.3e-4	Carbon lost from CWD per year was calculated using decay rate equations from Hérault et al., (2010). Assuming 75 % of decayed CWD is respired (Chambers et al., 2001) the time to decay whole CWD pool based on 18 % of carbon lost to soil pool was then calculated.
Respired fraction of A_f	R_{Ff}	Fraction	0.50	0.30	0.82	0.78 (0.96)	0.77 (0.93)	0.79 (0.99)	Default assumption for fraction of respired carbon in ACM
Respired fraction of A_w	R_{Fw}	Fraction	0.50	0.30	0.82	0.61 (0.80)	0.57 (0.77)	0.66 (0.83)	Default assumption for fraction of respired carbon in ACM
Respired fraction of A_{fr}	R_{Ffr}	Fraction	0.50	0.30	0.82	0.46 (0.33)	0.36 (0.29)	0.53 (0.37)	Default assumption for fraction of respired carbon in ACM
Respired fraction of A_{cr}	R_{Fcr}	Fraction	0.50	0.30	0.82	0.89 (0.65)	0.61 (0.44)	0.97 (0.84)	Default assumption for fraction of respired carbon in ACM
Respired fraction of C_{lit}	R_{Flit}	Fraction	1.0e-3	4.7e-4	2.1e-3	9.2e-4	4.9e-4	1.7e-3	Set to ACM default
Respired fraction C_{cwd}	R_{Fcwd}	Fraction	2.0e-4	9.4e-5	4.2e-4	2.3e-4	1.7e-4	2.9e-4	Carbon lost from CWD per year was as for D_{cwd}. Assuming 75 % of decayed CWD is respired (Chambers et al., 2001), the fraction of carbon respired from the CWD pool per day was calculated.
Respired fraction C_{som}	R_{Fsom}	Fraction	1.0e-4	4.7e-5	2.1e-4	6.4e-5	5.2e-5	7.8e-5	Set to ACM default

4.4 Results

4.4.1 Model calibration & DA output

The SPA model provided a good representation of the seasonal gross primary productivity of this ecosystem. The GPP values predicted by SPA matched the values and seasonal patterns reported by Bonal et al., (2008; Figure 4.3) with a root mean squared error (RMSE) of 0.24 g C m^{-2} d^{-1}. Following the optimization of the 10 parameters in ACM, ACM was able to closely reproduce the daily GPP values simulated in SPA (RMSE=0.05 g C m^{-2} d^{-1}).

All parameter steps and acceptance were performed in log normal space by the DA; therefore we assume that the distribution of posterior parameters and the model output from the DA will be log normally distributed. The posterior parameter values and ranges were calculated as the 50^{th}, 15.9^{th} and 84.1^{th} quantiles of the 1 million accepted parameter combinations. These quantiles are equivalent to the mean and plus and minus one standard deviation for a log normal distribution. For data storage purposes we randomly selected and saved the data output from 1000 of the 1 million accepted model runs. The 50^{th}, 15.9^{th} and 84.1^{th} quantiles were calculated for each output variable form the 1000 runs as an estimation of the mean and standard deviation.

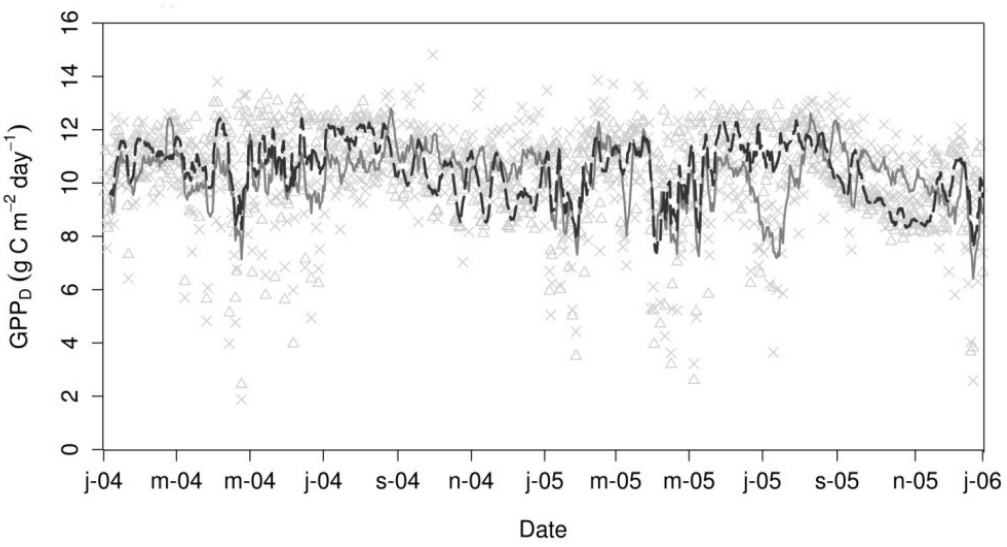

Figure 4.3: Comparison of the GPP from the SPA model run at the Paracou site with the GPP calculated from the eddy covariance data collected at the site from 2004–2005 and published in Bonal et al., (2008). Light-grey crosses indicate daily GPP (g C m^{-2} d^{-1}) from Bonal et al., (2008) and light-grey triangles the equivalent from SPA. The lines show the six-day running mean from SPA (dark-grey dotted line) and Bonal et al., (2008; light-grey solid

4.4.2 Seasonal changes in parameters

The standard deviation for four of the parameters, turnover rate of foliage (T_f ; wet season), turnover rate of fine roots(T_{fr}; wet season), allocation to fine roots ($A_{fr;}$ dry season), and respiration fraction from foliages ($R_{Ff;}$ dry season), had ranges which were outside of the ranges of the priors (Table 4.1). The outcome of the DA analysis showed distinct seasonality in nine of the parameters related to the autotrophic pools which were allowed to vary from wet to dry season (Figure 4.4): allocation to foliage (A_f), fine roots (A_{fr}) and wood (A_w), turnover rate of foliage (T_f), and fine roots (T_{fr}), and the respired fraction of carbon allocated to foliage (R_{Ff}), wood (R_{Fw}), fine roots (R_{Ffr}) and coarse roots (R_{Fcr}). These seasonal changes in carbon allocation in the DA were a result of a 27.2±2.3 % dry season decrease in the A_w parameter, a 21.9±1.4 % dry season decrease in the A_f parameter and a 52.2±8.0 % dry season increase in the A_{fr} parameter in the dry season (Table 4.1; Figure 4.4).

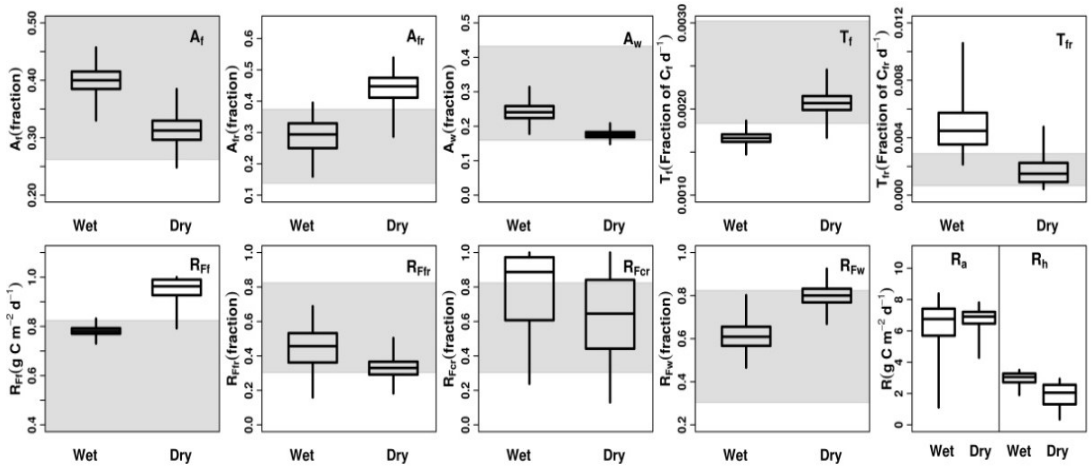

Figure 4.4: Box plots of the accepted parameters for allocation to foliage (A_f), allocation to fine roots (A_{fr}), allocation to wood (A_w), turnover rate of foliage (Tf), turnover rate of foliage (T_{fr} and the respiration fraction of carbon allocation to foliage (R_{Ff}), to fine roots (R_{Ffr}) to coarse roots (R_{Fcr}) and to wood (R_{Fw}), for the wet and dry season. The centre line shows the 50th quantile, and the box the 15.9th and the 84.1th quantiles, and the lines the maximum and minimum of the posterior distribution of the parameters. The grey shaded area shows the standard deviation on the prior. The final panel (lower right) shows the autotrophic respiration (R_a, g C m^{-2} d^{-1}) in the wet and dry season (left) and the heterotrophic respiration (R_h) in the wet and the dry season (right).

The data assimilation analysis showed that the dry season increase in the allocation to fine roots was balanced by a substantial decrease in the fine root turnover rate (66.7±34.0 %), which was equivalent to the fine root residency time increasing from approximately 2.5 years in wet season to 4.1 years in dry season. The turnover rate of coarse roots also decreased (24.8±18.7 %), however the uncertainty on this change was high. In contrast, the turnover rate of foliage increased 24.5±1.2 % in dry season, however there was only a small change in the turnover rate of wood (Table 4.1).

The fraction of the carbon allocated to foliage increased from wet (0.78±0.01) to dry season (0.96±0.31). The fraction of carbon allocated to wood which was respired showed a similar magnitude increase from wet (0.61±0.25) to dry season

(0.80±0.03). For both coarse roots and fine roots there was a 27 % reduction in parameter which determined the fraction of respired carbon in the dry season (Table 4.1). Despite the change in the fraction of respired carbon which is allocated to the fine and coarse roots, there was little seasonal change total in fine root (-0.01±0.23 g C m^{-2} d^{-1}) and coarse root (0.15±0.22 g C m^{-2} d^{-1}) respiration output from the model.

The assimilation constrained the majority of the parameters relative to their prior distributions. The wet season turnover rate of coarse roots and litter (T_{cr}; D_{lit}) and the initial values of the C_{fr}, C_{cr}, C_{cwd}, and C_{som} pools were the only parameters that were not constrained relative to the size of their prior ranges. With the exception of T_w, all of the parameters associated with the foliage and wood pools were tightly constrained (standard deviation <10% of the mean; Table 4.1). The DA analysis did predict high uncertainty (standard deviation ≥ 40 % of the mean) for the A_{cr}, (wet season only), T_{cr}, T_{fr} (dry season only), D_{lit}, D_{cwd}, R_{Flit} parameters. Despite high uncertainties on these parameters, the DA analysis tightly constrained (standard deviations <10 % of the mean) the GPP, R_{eco}, R_a, R_h and CUE (Table 4.2).

4.4.3 Comparison of the DA to the prior model run

The mean model bias between the data and the prior run was high for LAI (+10.01 m^3 m^{-3}), litter-fall (+1.37 g C m^{-2} d^{-1}) and NEE (-1.37 g C m^{-2} d^{-1}; Table 4.2). The DA analysis reduced the carbon allocated to foliage and the fraction of this carbon which was respired (Table 4.1); this significantly reduced the biases associated LAI and litter-fall in the priors run (Table 4.3, Figure 4.5). The DA predicted a greater increase of respiration from dry to wet season than the prior run; the decrease in wet season carbon storage which resulted, caused greater wet season NEE which reduced the bias associated with the simulated NEE in prior run (Table 4.2). The prior run

consistently overestimated the respiration from soil in wet and dry season by approximately 1.05 g C m^{-2} d^{-1}; the DA reduced this overestimation (Table 4.2) through reducing the fraction of the soil organic matter pool which was respired (Table 4.1). The biases between the woody biomass in the prior run and the data were 2293.3 g C m^{-2}; however a reduction in the carbon allocated to wood by the DA reduced this bias to 103.0 g C m^2 (Table 4.1 and 3). The normalised biases between the prior run and the data on respiration from wood and respiration from CWD were low (2.7% and 5.2%, respectively; Table 4.2); however, dry season reductions in the allocation to wood by the DA still improved the dry season representation of wood respiration (Figure 4.5, Table 4.2). Similarly, an increase in the turnover rate of the CWD pool reduced the bias associated with the prior run and the R_{cwd} data. R_f was the only factor for which the DA increased the bias with the data from -0.14 g C m^{-2} d^{-1} in the prior run to 0.6 g C m^{-2} d^{-1}.

Table 4.2: The bias between the measured values for respiration from foliage (R_f), respiration from wood (R_w), respiration from soil R_s respiration from CWD (R_{cwd}), woody biomass (C_w), leaf area index (LAI), litter-fall (Lf) and net ecosystem exchange (NEE), and the median data assimilation run and the priors run, calculated as the mean of the modelled values minus the measured values. The values in brackets show this error normalised by the mean model value, so that bias between variables can be compared.

Variable	**Mean bias DA run**		**Mean bias prior run**	
R_f (g C m^{-2} d^{-1})	0.6	**(21.54%)**	-0.14	**(-4.97%)**
R_w (g C m^{-2} d^{-1})	0	**(0.05%)**	0.04	**(2.69%)**
R_s (g C m^{-2} d^{-1})	0.51	**(13.95%)**	1.05	**(28.67%)**
R_{cwd} (g C m^{-2} d^{-1})	0.01	**(1.4%)**	0.02	**(5.16%)**
C_w (g C m^{-2})	209.07	**(0.93%)**	2293.3	**(10.15%)**
LAI (m^2 m^{-2})	0.25	**(4.01%)**	10.01	**(159.17%)**
L_f (g C m^{-2} d^{-1})	0.21	**(23.11%)**	1.35	**(148.85%)**
NEE (g C m^{-2} d^{-1})	0.19	**(37.98%)**	-1.37	**(279.72%)**

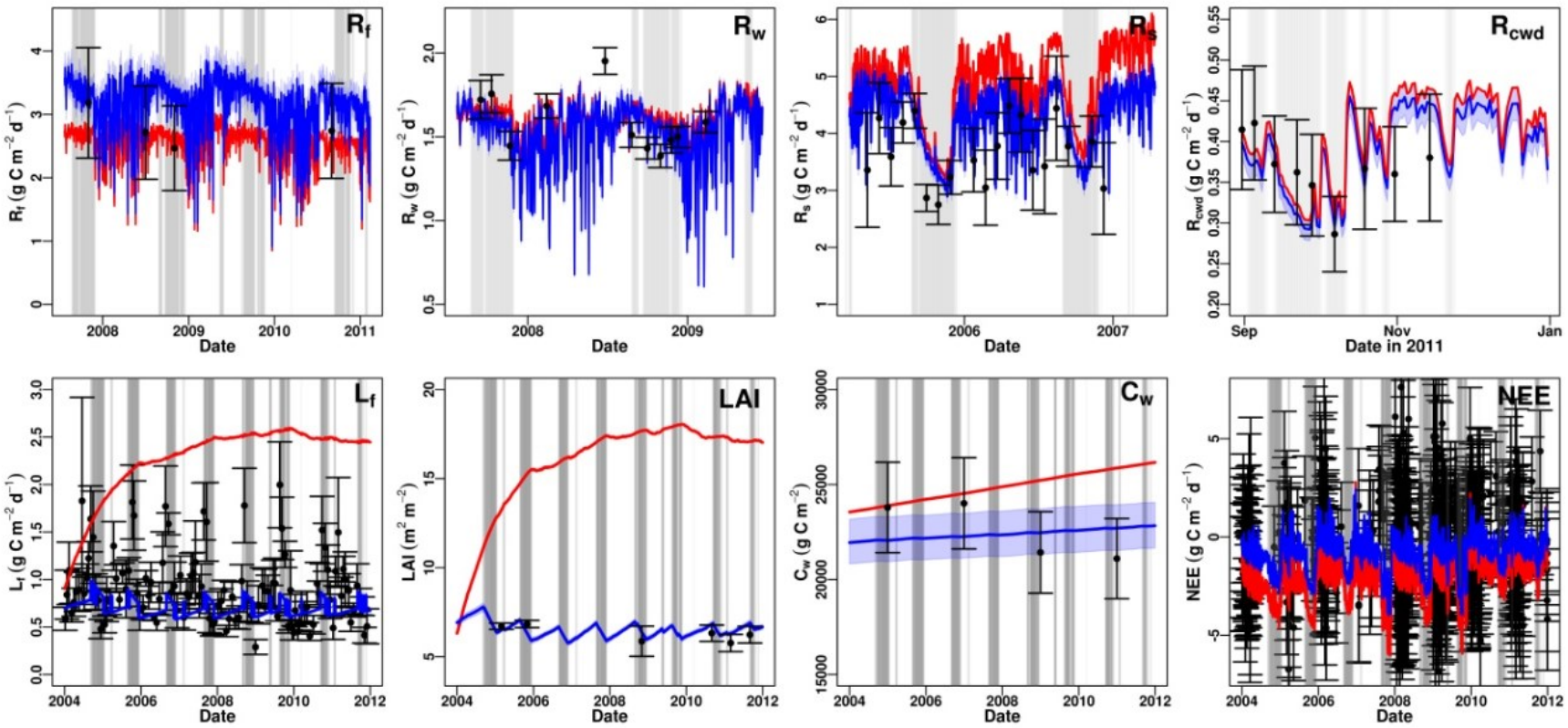

Figure 4.5: Comparison of data (black points, shown with standard error bars) for foliage respiration (R_f), woody respiration (R_w), soil respiration (including litter and roots; R_s), coarse dead wood respiration (R_{cwd}; year 2011), litter-fall (L_f), leaf area index (LAI), wood biomass (C_W) and net ecosystem exchange (NEE). Median results (blue line) with the 15.9th and the 84.1th quantiles (blue shaded area) shown for the results of the DA. The red line shows the results of the prior run with DALEC-fg. The grey shaded area indicates the periods classified as the dry season.

4.4.4 Seasonal change in R_a and R_h

Mean annual autotrophic respiration (R_a) from the DA analysis was 2415±50 g C m^{-2} yr^{-1}, more than twice the size of the annual heterotrophic respiration (R_h; 1000±39 g C m^{-2} yr^{-1}; Table 4.3). Mean annual R_a from the DA was comprised of 48.0±2.4% R_f, 22.5±0.6 % R_w, 20.8±2.3 % R_{fr}, and 8.7±2.3 % R_{cr}. Mean annual modelled R_h was comprised of 73.5±6.2 % R_{som}, 13.1±3.1 % R_{lit}, and 13.4±0.8 % R_{cwd} (Table 4.3). R_h was reduced by 36.0±1.4 % from wet to dry season (Table 4.3). All heterotrophic respiration sources from the DA had a reduction of mean daily wet to dry season respiration of between 35-37 %, and the contribution of each component to the reduction in R_h in dry season was proportional to the fraction each flux contributed to the annual sum of R_h. The change in mean daily R_a from wet to dry season was significantly smaller than R_h (+4.6±0.1 %; Table 4.3). The positive change in R_a was mostly caused by a small increase in foliage and coarse root respiration in dry season (0.14±0.23 g C m^{-2} d^{-1} and 0.15±0.2 g C m^{-2} d^{-1}, respectively), and although small, this change served to offset part of the decrease in R_h.

4.4.5 Seasonal changes in carbon balance

The DA reduced R_{eco} by 0.78±0.20 g C m^{-2} yr^{-1} from wet to dry season; the dry season reduction in R_h (1.09±0.14 g C m^{-2} d^{-1}) was actually greater than the reduction in R_{eco} as it also offset the dry season increase in R_a (Table 4.3). GPP increased from wet to dry season by 0.79±0.07 g C m^{-2} yr^{-1}. The combined effect of increasing GPP and reductions in R_{eco} caused a significant reduction in NEE from -0.54±0.12 g C m^{-2} yr^{-1} in wet season to -2.11±0.14 g C m^{-2} yr^{-1} in dry season. As the reduction in R_{eco} was roughly equal to the change in GPP both were almost equally responsible for this change. The dominance of seasonal changes in R_{som} in changing R_{eco} meant that

R_{som} alone caused 36.6±12.6 % of the seasonal change in NEE.

The data assimilation predicted that mean annual carbon use efficiency (CUE) was 0.36±0.02 (Table 4.3). During the wet season the CUE was 0.35±0.02, however during the dry season this value rose to 0.37±0.02, suggesting that this forest is slightly more efficient at using carbon in the dry season. The increase in dry season CUE was caused because R_a did not increase as much as GPP in the dry season (Table 4.3), causing a greater amount of net carbon investment in the dry season.

4.5 Discussions

4.5.1 Overview

The 36 model parameters estimated using the DA produced a better fit to the data than using the prior estimates of parameters (Table 4.2; Figure 4.5). In agreement with Bonal et al., (2008) our results suggest that this forest is on average a sink of carbon, however we demonstrate that in fact the forest sequesters carbon four times faster in the dry season, than in the wet season (Figure 4.5). Our study is unique in that it can it can with a high degree of certainty directly attribute 50% of this change to an increase in GPP and the other 50% to changes in reduced heterotrophic respiration in response to drying soils (Table 4.3). We therefore demonstrate that seasonal changes in model parameters are important to correctly simulate the carbon balance of tropical forests.

Table 4.3: The mean carbon pools and fluxes (allocation, net primary production (NPP) and respiration) predicted by the DA analysis for study site from 2004-2011. Data is shown as mean values for wet and dry season and as mean annual sums. The values are calculated from 1000 randomly selected DA model runs and shown alongside the standard deviation across these model runs (SD).

	WET SEASON		**DRY SEASON**		**ANNUAL**	
	Mean	**SD**	**Mean**	**SD**	**Sum**	**SD**
Allocation	***g C m^{-2} d^{-1}***				***g C m^{-2} yr^{-1}***	
A_f	4.01	0.19	3.42	0.18	1413.1	54.9
A_w	2.36	0.12	1.88	0.07	818.5	38.5
A_{cfr}	3.04	0.22	4.84	0.22	1272.6	61.7
A_{cr}	0.64	0.14	0.71	0.18	252.5	43.7
NPP	***g C m^{-2} d^{-1}***				***g C m^{-2} y^{-1}***	
NPP_f	0.88	0.04	0.14	0.11	254.2	4.7
NPP_{fr}	1.69	0.19	3.43	0.17	771.3	55.3
NPP_{cr}	0.10	0.06	0.09	0.08	41.7	20.2
NPP_w	0.88	0.12	0.36	0.06	274.4	37.9
Respiration	***g C m^{-2} d^{-1}***				***g C m^{-2} yr^{-1}***	
R_f	3.13	0.18	3.27	0.15	1158.9	54.2
aR_w	1.48	0.03	1.53	0.03	544.2	8.5
R_{fr}	1.42	0.17	1.40	0.15	501.3	53.7
R_{cr}	0.49	0.16	0.64	0.14	210.8	54.9
R_{lit}	0.40	0.09	0.26	0.06	130.8	30.2
R_{cwd}	0.41	0.02	0.26	0.01	134.5	6.5
R_{som}	2.23	0.16	1.43	0.11	735.0	54.6
Pools	***g C m^{-2}***				***g C m^{-2}***	
C_f	398	8	397	8	398	8
C_w	22376	1225	22362	1217	22373	1223
C_{fr}	465	57	520	52	480	56
C_{cr}	2842	717	2841	714	2842	717
C_{lit}	524	63	530	63	525	64
C_{cwd}	2181	364	2179	364	2181	364
C_{som}	29579	5668	29462	5676	29550	5670
Ecosystem fluxes	***g C m^{-2} d^{-1}***				***g C m^{-2} yr^{-1}***	
NEE	-0.54	0.12	-2.11	0.15	-341.4	36.3
GPP	10.09	0.05	10.87	0.05	3756.7	19.1
R_{eco}	9.55	0.13	8.77	0.15	3415.3	38.5
R_a	6.53	0.17	6.83	0.14	2415.1	49.7
R_h	3.02	0.12	1.93	0.08	1000.2	39.1
CUE	0.35	0.02	0.37	0.01	0.36	0.02

4.5.2 Allocation and respiration from leaves, stems and roots

Of annual GPP equal proportions were allocated to foliage (37.7±1.5 %) and fine roots (33.9±1.7 %). The remaining was mostly allocated to stem wood (21.8±1.0 %) and 6.7±1.2 % was allocated to coarse roots. This roughly equal division between foliage, wood (stems and coarse roots) and fine roots is in agreement with the findings of Malhi et al. (2011), who studied allocation patterns at sites across the Amazon. Changes in allocation patterns were caused by changes in allocation from wood and foliage to fine roots (Figure 4.4; Table 4.1 & 3). When changes in respiration are also considered the net investment of carbon into foliage and wood (NPP_f NPP_w) increased by 0.75±0.11 g C m^{-2} d^{-1} and 0.52±0.14 g C m^{-2} d^{-1} respectively, in the wet season contrasting NPP_{fr} which increased by 1.74±0.25g C m^{-2} d^{-1} in the dry season (Table 4.3). We therefore reject hypothesis 1a, that seasonal allocation patterns are constant between seasons and suggest that this system favours carbon investment in roots in the dry season and carbon investment in stems and leaves in the wet season. Previous studies at this site have shown that woody productivity is greater in the dry season than the wet season (Wagner et al., 2012). However, the dry season increase in NPP_{fr} disagrees with a study in north east Brazil which found an overall decrease in dry season root growth (Metcalfe et al., 2007), despite high spatial heterogeneity. A lack of data to explicitly constrain the allocation and turnover of the root pool in this study caused the standard deviations on the root parameters, from the DA, particularly root turnover rate, to have higher error than parameters associated with the wood and foliage pools (Table 4.1). More data and certainty from field studies is therefore necessary to enable models to provide a tighter constraint on the seasonal changes in patterns of root dynamics.

The DA predicted a small increase in dry season R_a of 0.30±0.22 g C m^{-2} d^{-1}, which

was caused by a small increase in both R_f and R_{fr}. The change is very small relative to the size R_a and considering the error on this change, which was 74 %. When this error is considered we accept hypothesis 1b, that there is only likely to be small variations in the components R_a.

4.5.3 Seasonality changes in the carbon balance.

Average GPP was 341±36 g C m^{-2} yr^{-1} greater than $R_{eco.}$ The DA therefore suggests that this forest is a greater carbon sink in wet (-0.54±0.12 g C m^{-2} yr^{-1}) and dry season (-2.1±0.15 g C m^{-2} yr^{-1}) than has been estimated by previous studies (Bonal et al., 2008: 0.1 g C m^{-2} yr^{-1} (wet season) 0.35-0.70 g C m^{-2} yr^{-1} (dry season)). Bonal et al., (2008) may underestimates the carbon sink because of the assumption made when processing eddy covariance data; for example assuming that daytime ecosystem respiration is equal to NEE measured at night. The model showed with reasonable certainty that the strength of this sink increased by approximately four times from wet to dry season (Table 4.3; Figure 4.5). The increased strength of the sink was caused by an increase of GPP by 0.79±0.07 g C m^{-2} d^{-1} and a decrease of 0.78±0.20 g C m^{-2} d^{-1} in R_{eco}. The effect of decreasing respiration and increasing GPP was therefore equally important for the seasonal change in the carbon balance of this ecosystem. All of the seasonal reduction in R_{eco} was caused by a reduction in R_h, which was large enough to cause the decrease R_{eco} and compensate for the 0.30±0.22 g C m^{-2} d^{-1} increase in R_a. We accept hypothesis 2a finding that the change in R_h between wet and dry season was greater than the change in R_a and GPP (Table 4.3), and therefore caused the greatest change to the ecosystem carbon balance.

Annual R_{eco} was 70.7±1.7 % R_a and 29.3±1.2 % R_h. These values are similar to

estimates from bottom up carbon balance studies in eastern Amazonian forests (Malhi et al., 2009; Metcalfe et al., 2010) which suggest that heterotrophic respiration is close to half of autotrophic respiration at the ecosystem level. The ratio R_h to R_a decreased from R_h being half of R_a in the wet season (0.46 ±0.02) to being less than a third of it in dry season (0.28±0.01; Table 4.3, Figure 4.4). The ratio changed between seasons because the dry season reduction of R_h was greater (36.0±1.5 %) than the increase in R_a (4.6±0.1 %). We accept hypothesis 2b that R_a is consistently greater than R_h, however we find that the ratio between R_h and R_a is reduced in dry season.

4.5.4 Quantifying seasonal changes in carbon use efficiency

Mean annual carbon use efficiency (CUE) was 0.36±0.02. This value is lower than the universal value of 0.5 proposed by Waring et al., (1998) and closer to the CUE values proposed by Malhi et al., (2009) for two undisturbed old growth forests in the eastern Amazon (0.34±0.10 and 0.34±0.07). Our study does, however demonstrate that CUE is not completely stable between wet and dry season (Table 4.3). Our study shows that there is a small, but significant, increase in CUE between wet and dry season (5.38±0.3 %). The increase is cause by increases in dry season GPP being accompanied by smaller changes in R_a (Table 4.3) demonstrating that forest is slightly more efficient at using carbon in the dry season. As the change in CUE is small we accept hypothesis 3 that there is low seasonal variation in the efficiency of the carbon use of this forest.

4.5.5 Model-data inconsistencies

The model prediction for respiration from foliage was similar to values found at other sites in the eastern Amazon (Malhi et al., 2009; Metcalfe et al., 2010; da Costa et al., in press). However, the mean bias from the DA scheme (0.60 g C m^{-2} d^{-1}) was slightly greater than for the prior run (-0.14 g C m^{-2} d^{-1}; Table2). The increase in this bias may have been caused by a data inconsistency between multiple sources of data, which resulted in the DA not being able to improve the fit of all the data. Such data inconsistency may arise from errors associated with scaling up measurements to represent plot level fluxes. We suggest that this is likely because the carbon allocated to, lost and respired from foliage were tightly constrained (Table 4.1). Similarly the DA was also unable to fit the high litter-fall values (Figure 4.5), and although substantially improved from the prior run the bias associated with litter-fall remained high (Table 4.2). The litter-fall data showed a pulse of litter-fall for one to two months in the dry season; however the LAI data showed no change. The data suggest that the forest goes through a dry season leaf flush event where old leaves are lost and quickly replaced with new leaves. The timing and causes of such peak litter-fall events can be highly variable between forests and remains poorly understood in the tropics (O'Brien et al., 2008; Chave et al., 2010). Consequently the mechanism within models is not adequate to simulate such phenomena and therefore litter-fall patterns remain difficult to parameterise correctly in models of tropical ecosystems (Verbeeck et al., 2011).

4.6 Conclusions

Utilising the information provided by nine orthogonal data sets, the DA scheme used

in this study provides an optimal estimation of the seasonal changes in the carbon balance of a tropical forest site. We find that the mean daily carbon storage (NEE) is close to four times greater in dry season than wet season. A dry season reduction in R_{eco} and increase in GPP contributed equally to the net change in NEE between wet and dry season. Changes in heterotrophic respiration in response to reduction in soil moisture content were responsible for all of the dry season reduction in R_{eco}. In contrast R_a demonstrated a slight increase in the dry season. The smaller total increase in R_a in the dry season relative to GPP caused a slight increase in the CUE of this ecosystem.

The model parameterisation following the DA appears to accurately capture patterns of allocation and respiration previously observed in Amazonian forests. The DA does however produce high uncertainty on most of the parameters associated with the root pools. This study therefore suggests that obtaining more data on seasonal change in the turnover rate of roots, and the seasonal changes in root growth and respiration is important to improve the constraint on seasonal change in the carbon balance of tropical forests.

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Chapter 5: A model inter-comparison to explore the temperature sensitivity of a tropical forest experiencing drought.

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LR: Study design, SPA model simulation, data analysis, paper writing. AH: Study design, SiB model simulation. BJC: Study design, CLM model simulation. TLP: Study design, ED model simulation. PB: Study design, metrological data. NL: Study design, Metrological data. YM: Study Design. SS: Study Design. PRM: Study Design. PM: Data anylsis and Study design. MW: Study design, Data analysis, Paper writing.

5.1 Abstract

Amazonian forests are dynamic and have the capacity to switch from a sink of atmospheric carbon to a source with changes in climate regularly observed over timescales of less than a year. However, how these forests will respond to the expected changes in temperature and precipitation over the coming decades and centuries remains unclear. In this study we compare leaf to canopy scale responses of four sophisticated vegetation models (CLM-DGVM3.5, ED2, SiB3 and SPA2) to changes in air temperature and precipitation in the eastern Amazon.

Our results demonstrate that although all the models simulate reduced productivity with increasing temperature and drought, there was high variability in the sensitivity of leaf and canopy scale fluxes to these changes. Depending on the model, simulated gross primary productivity (GPP) was restricted by stomatal conductance at high temperatures either due to soil or atmospheric water stress. We demonstrate that between the models the equivalent temperature rise necessary to simulate the same average reduction GPP as a 50 % reduction in wet season precipitation ranged between 5-17.5 °C. We find no consensus between the vegetation models as to whether there is a stronger sensitivity to drought or temperature; instead two of the models demonstrate a stronger sensitivity to temperature and the two other models a stronger sensitivity to drought.

To be confident in our predictions of the impacts of climate change in Amazonia, we must find some consensus between the models used to make such predictions. This study demonstrates that the models we tested generally responded in differently ways to changes in temperature and drought when simulating an Amazonian forest, and

when the models did predict similar responses it was generally for different reasons. We highlight the key areas of inter-model uncertainty at both the leaf and the canopy scale and suggest ways forward to reduce such uncertainties.

5.2 Introduction

Tropical forests account for 55 % of global forest biomass (Pan et al., 2011) and are an integral part of the global carbon cycle. Amazonia contains the world's largest expanse of humid tropical forest (Eva et al., 2004). Old-growth Amazonian forests are an important sink of atmospheric carbon and are estimated to be accumulating 0.39±0.26 Pg C yr^{-1} (Gloor et al., 2012). However, during the period of 2005-2009, a strong drought caused these forests to switch from having a net uptake of carbon, to having a net release of 0.66±0.23 Pg C yr^{-1} (Gloor et al., 2012). The large quantity of carbon stored in the Amazon forest (~69-102 Pg C; Saatchi et al., 2007) and its dynamic nature caused by high turnover rates, means even very small changes in the processes involved in carbon uptake and storage can cause significant changes to the carbon balance of this system.

Recent modelling studies have shown that mid-range IPCC scenarios for future rises in atmospheric carbon dioxide (CO_2) levels are likely to cause increases in temperature and reductions in rainfall across Amazonia (Christensen et al, 2007; Malhi et al., 2009; Jupp et al., 2010; Marengo et al., 2012). However, recent review articles have highlighted the uncertainties regarding the response of tropical forests to warming temperatures (Corlett, 2011; Reed et al., 2012; Wood et al., 2012) and drought (Fisher et al., 2008; Meir et al., 2008; Meir and Woodward, 2010). Uncertainties in the coupling between the climate and vegetation and the associated impact of changes in temperature and precipitation, combined with the uncertainty from differing model predictions (Friedlingstein et al., 2006; Sitch et al., 2008; Galbraith et al., 2010), currently limit our ability to predict future changes in both vegetation and climate (Meehl et al., 2009).

In some modelling studies the combined effects of rises in temperature and reductions in precipitation have caused substantial reductions in the predicted forest cover of Amazonia (Betts et al., 2004; Cox et al., 2004; Huntingford et al., 2008). However, the ecosystem responses of models to multi-factor changes in climate can be hard to interpret because of complex nonlinear process responses (Zhou et al., 2008), which can vary substantially between vegetation models with different model structures. A study using four vegetation models (CENTURY, LPJ, ORCHIDEE, TECO) demonstrates that halving precipitation significantly amplifies the negative effect caused by temperature rise on net primary productivity at a forest in the eastern Amazon (Luo et al., 2008). In this study the sensitivity of each model to the simultaneous change in precipitation and temperature varied substantially, therefore creating uncertainty in the current ability to predict future change. In a separate study the effect of temperature rises on changes in modelled tropical forest biomass has been found to be greater than the effect of reduced precipitation in a study using three dynamic vegetation models (HYLAND, TRIFFED, LPJ; Galbraith et al., 2010). Previous modelling studies validated with data at a drought experiment in the eastern Amazon have shown that a 50 % reduction in precipitation with no temperature changes caused an annual reduction of GPP of 13% over a 2 year period (Fisher et al., 2006; Fisher et al., 2007). The effect of reduced water availability and increasing temperatures therefore remains variable and poorly quantified in Amazonia (Luo et al., 2008; Sitch et al., 2008; Galbraith et al., 2010). The response of ecosystem fluxes to changes in temperature and precipitation will be directly related to how leaves respond to changes in temperature and available soil moisture. These relations have, however, been poorly investigated within models.

Changes in precipitation and temperature can affect the carbon cycle of tropical forests in multiple ways, and over different time scales. An example of the positive and negative feedback effects on the carbon cycle of a tropical forest, which may result from a rise in temperature and a reduction in precipitation, are shown in Figure 5.1. In the short term increasing air temperature alters enzyme activity causing biochemical changes and alterations to the maximum rates of RuBP carboxylation and electron transport (V_{cmax} and J_{max}) inside the leaf. Temperature increases can have both a positive or a negative effect on V_{cmax} and J_{max}, as enzyme activity rates will generally increase with rising temperature until a threshold is reached after which damage will occur in the leaf (Figure 5.1). Similarly increases in temperature, and decreases in precipitation will both increase vapour pressure deficit (VPD). Increased VPD causes greater atmospheric water demand which can reduce stomatal conductance and therefore photosynthesis rates (Figure 5.1). Over longer periods, increased VPD can also cause greater evaporation and also reduce soil water content (SWC) as would reduced precipitation. Reduced SWC will reduce the supply of water to the leaf, and cause further reductions in stomatal conductance (Figure 5.1). The reductions in photosynthesis from increased temperature or reduced precipitation will directly reduce gross primary production (GPP). Reductions in photosynthesis can cause leaf loss reducing leaf area index (LAI) and resulting in a positive feedback. Autotrophic respiration can be both positively and negatively affected by increased temperature, but generally decreases with GPP. In the tropics heterotrophic respiration has been found to increase with increasing temperature, but decrease with reduced water availability (Sotta et al., 2004; Sotta et al., 2007; Bonal et al., 2008; Meir et al., 2008).

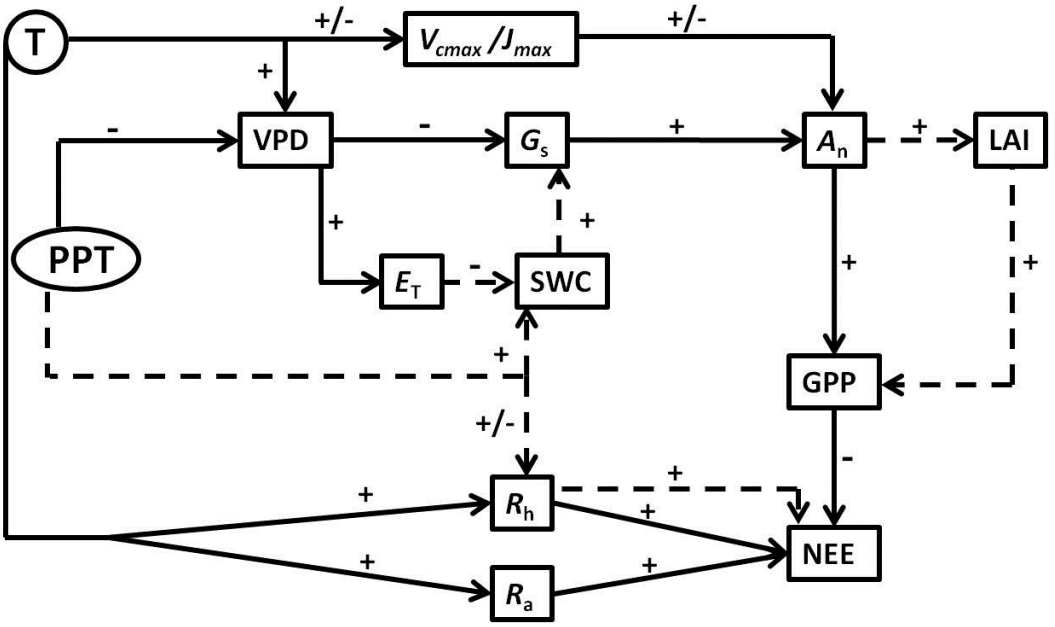

Figure 5.1: Schematic diagram showing the effect of air temperature (T) and precipitation (PPT) on the carbon cycle of a tropical forest, with unchanged irradiance, including the effects on: vapour pressure deficit (VPD), evapo-transpiration (E_t), stomatal conductance (g_s), soil water content (SWC), net photosynthesis (A_n), leaf area index (LAI), the maximum rates of RuBP carboxylation and electron transport (V_{cmax} and J_{max} respectively), autotrophic respiration (R_a) heterotrophic respiration (R_h), gross primary productivity (GPP), and net ecosystem exchange (NEE). + signs indicate a positive effect, - signs indicate a negative effect, and +/- indicate the possibility of a positive or a negative effect. Solid arrows represent responses which occur over short timescales of minutes to hours, whereas dashes arrows represent responses which can occur over longer timescales from days to months.

The feedbacks shown in Figure 5.1 are complex and many of the responses are likely to be thresholds rather than continuous responses, due to the capacity of forests to buffer themselves against short term changes in climate. Studies using models and eddy covariance data at sites in the Amazon have shown that Amazonian forests tend to maintain GPP in the dry season when temperatures are higher and there is reduced soil water availability (Saleska et al., 2003; Fisher et al., 2006; Fisher et al., 2007; Hutyra et al., 2007; Baker et al., 2008; Bonal et al., 2008). This sustained GPP might be caused by trees accessing water with deep roots (Nepstad et al., 1994; da Rocha et al., 2004; Oliveira et al., 2005). Remote sensing data have however, suggested that Amazonian forests are more productive in the dry season because of increased direct canopy illumination, new leaf growth and greater LAI (Huete et al., 2006; Myneni et al., 2007; Saleska et al., 2007) although the results of such studies are still debated (Anderson et al., 2010; Asner and Alencar, 2010; Samanta et al., 2010; Samanta et al., 2012). Similarly the response of Amazonian forests to rises in temperature is also subject to debate. Some studies suggest that tropical forest growth and productivity have continued to increase with rises in air temperature (Lloyd and Farquhar, 2008; Phillips et al., 2008; Lewis et al., 2009). In contrast, other studies have found that the productivity of tropical forests trees and leaves responds negatively to small increases in above average ambient air temperatures (Clark et al., 2003; Goulden et al., 2004; Feeley et al., 2007; Doughty and Goulden, 2008; Doughty, 2011). It seems therefore that both the structural and physiological response of Amazonian forests to changes in temperature and precipitation remain unresolved and further research is required in both field and modelling studies to provide a greater understanding.

This study explores the processes underlying the sensitivity of four vegetation

models (CLM3.5, ED2, SiB3, SPA2) to changes in temperature and precipitation at the Tapajós forest site in eastern Brazil. In all models we simulate first an ambient and then a 50 % reduction in the incoming precipitation during the wet season from 2000-2006, linked to a -5 °C, 0 °C, +2 °C, +4 °C, or +6 °C change to the ambient air temperature. We compare the temperature sensitivity of the modelled carbon fluxes to observed temperature sensitivities at the canopy scale. We use this model experiment to address the following questions and associated hypotheses:

Q1: How sensitive to changes in air temperature are the modelled direct (biochemical) and indirect (stomatal) physiological controls on photosynthesis?

H1: Models will demonstrate a greater influence of indirect temperature controls on photosynthesis.

H2: At high leaf temperatures stomatal conductance will be restricted as a result of the model's soil water stress functions preventing high loss of water through evapo-transpiration.

Q2: How sensitive is the modelled carbon balance of this forest to the effects of temperature change on GPP, LAI and ecosystem respiration?

H3: The temperature response of net ecosystem exchange is determined by GPP and not ecosystem respiration.

H4: LAI will show significant reductions with increases in air temperature in models which simulate dynamic LAI and this will, in turn, lower GPP.

Q3: Are vegetation models more sensitive to increases in air temperature or

decreases in precipitation?

H5: There is an interaction between temperature and drought effects amongst all models.

H6: Vegetation models will simulate a stronger temperature response than drought response in the Amazon under scenarios of predicted change for the 21st century.

5.3 Materials and Methods

This study site was selected as part of a wider model inter-comparison project which aims to explore how well six vegetation models simulate two through-fall exclusion (TFE) experiments in the eastern Amazon (Christoffersen et al., in prep; Powell et al., in, prep). This study explores the temperature responses in four of these vegetation models (the Community Land Model , the Ecosystem Demography model, the Simple Biosphere model and the Soil-Plant-Atmosphere model) and how they respond to the 50 % reduction in wet season precipitation, as simulated at the TFE in the Tapajós national forest (TNF, 2.897 S, 54.952 W). This section will outline the study site and the set up of four vegetation models to simulate the site, alongside the experimental design to simulate changes in precipitation and air temperature.

5.3.1 Site

The TNF forest is located on an Oxisol, and has a mean annual precipitation of 2 m per year; the site is described in detail by Nepstad et al. (2002). This plot was

selected for this experiment because previously data has been collected on the temperature response of canopy level net ecosystem exchange (NEE; Doughty and Goulden, 2008) at this site, and therefore this data could be used as a comparison. Doughty and Goulden (2008) report the response of NEE measured from an eddy covariance tower on the site from July 2000 to July 2001, when light levels were above 1000 μmols m^{-2} s^{-1} (details of set-up and data processing methods are available in Doughty and Goulden (2008) and Goulden et al., 2004).

The framework for testing the effect of precipitation change was taken from the TFE experiment (Nepstad et al., 2002). The TFE experiment comprised of two 1 ha forest plots; one plot was a control plot and the second a TFE, where plastic panels were placed over the plot during the wet seasons (January-June) of 2000-2006 excluding 50 % of the rainfall (Nepstad et al., 2002). In this study we do not endeavour to make comparisons to the effect of the TFE, which has been done previously as part of this model inter-comparison project (Christoffersen et al., in prep; Powell et al., in, prep). Instead we use this existing drought simulation framework to explore the joint effects of temperature and precipitation change.

5.3.2 Model description

The four models used in this study span a range of complexity and canopy structures. A brief description of each of the models is given here in order of the complexity of the canopy structure; these details are summarised in Table 5.1. A more detailed description of each of the model canopy structures can be found in Appendix 2. The Simple Biosphere model 3 ((Sellers et al., 1992; Sellers et al., 1996; Baker et al.,

2008), hereafter reffered to as SiB) is a big-leaf model, which simulates the response of the top of the canopy to changes in environmental conditions and then integrates this response throughout the canopy according to a light and leaf nitrogen extinction coefficient. SiB can only simulate one plant functional type at a time, in this case tropical evergreen trees. The Community Land model 3.5 ((Oleson et al., 2008; Bonan et al., 2012), hereafter reffered to as CLM) is a also a big-leaf model, however it separates the canopy into a sunlit leaf fraction (leaves which receive both direct and diffuse light) and a shaded leaf fraction (leaves which receive only diffuse light), which change dynamically with sun angle and canopy light penetration. CLM simulates five dynamic plant functional types (PFTs: broadleaf tree, needle leaf tree, C3, C4 grass and bare ground); for these simulations the canopy in CLM remained > 95 % broadleaf tree unless specified otherwise. The Soil-Plant-Atmosphere model 2, (Williams, 1996; Williams et al., 2005) hereafter reffered to as SPA) is a layered canopy model, which was run with three canopy layers, each split into sunlit and shaded fractions, which like in CLM change dynamically with sun angle and canopy light penetration. SPA has a more complex light attenuation routine than CLM and SiB and models the light absorbed, reflected and re-absorbed by each canopy layer. Like SiB, SPA only models one PFT at a time, in these simulations this was tropical evergreen trees. The Ecosystem Demography model 2, (Medvigy et al., (2009), hereafter referred to as ED) is a gap model which separately models the stems of three groups of trees (early, mid and late successional) as well as grasses. ED is the only model which simulates stochastic tree mortality and forest gap formation. ED is therefore able to simulate a continuum of leaf light levels from fully shaded to fully sunlit and has the most realistic canopy light penetration scheme.

All of the models use similar versions of the leaf photosynthesis (A_n) equations, which were originally derived from Farquhar et al. (1980), Farquhar and Sharkey (1982), Kirschbaum and Farquhar (1984) and Collatz et al. (1991). Therefore in all models temperature can affect A_n directly through temperature response functions on the maximum rate of carboxylation of RuBP (V_{cmax}), the CO_2 compensation point, and the Michaleis-Menton constants (K_c and K_o; see Appendix 2 for further details). In SPA there is also a temperature response implemented on the maximum rate of electron transport (J_{max}). In all models changes in leaf temperature can also indirectly change A_n through changing the vapour pressure deficit at the leaf surface, which alters stomatal conductance (g_s). In all models, apart from SPA, g_s is modelled using a form of the Ball-Berry stomatal conductance model (Collatz et al., 1991; Appendix 2). SPA is unique in that it models stomatal conductance using a continuum between the soil and leaf water, in which it maximises g_s and photosynthesis at each time-step without letting leaf water potential drop below a critical level (-2.5 KPa; see Williams et al., 1996, for further detail).

SPA directly models the effect of water stress on photosynthesis through simulating changes in g_s according to changes in the soil to leaf water continuum (Williams et al., 1996). In contrast CLM, ED and SiB alter g_s using a water stress factor (β; a value of 0-1 where one indicates no water stress and 0 indicates complete water limitation). β declines as plant available soil water content and root biomass in the soil declines (see Appendix 2). ED also uses β directly on net photosynthesis (A_n), whereas CLM and SiB use β on V_{cmax} to down-regulate photosynthesis in water stress conditions. The model equations and full details of the effects of temperature and moisture on A_n are given in Appendix 2.

Table 1: Summary of the characteristics of each of the four vegetation models (CLM; ED; SiB; SPA).

	CLM	ED	SiB	SPA
No° of plant function types	5	4	1	1
Canopy	Big-leaf	Gap model	Big-leaf	Layered
Leaf Area index	Dynamic	Dynamic	Fixed	Dynamic
Division of sunlit and shaded leaves	Y (discrete division)	Y (division on a continuum)	N	Y(discrete division)
Simulation of water stress on A_n and g_s.	Water stress factor	Water stress factor	Water stress factor	Linked soil-leaf water potential/resistance model to g_s model.
Origin of photosynt-hesis model	Farquhar et al., (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)	Farquhar et al., (1980); Farquhar and Sharkey (1982); Collatz et al. (1991)	Farquhar et al., 1(980); Farquhar and Sharkey (1982) Collatz et al. (1991)	Farquhar et al., (1980); Kirschbaum and Farquhar (1984); McMurtrie et al. (1992).
Key model references	Oleson et al. (2008); Thorton and Zimmerman (2007); Bonan et al., (2012)	Medvigy et al., (2009)	Sellers et al., (1992); Sellers et al., (1996); Baker et al (2008).	Williams, (1996); Williams et al., (2005); Fisher et al., (2007)

5.3.3 Meteorological Data and Soil Properties

The models were run using hourly meteorological data (precipitation, air temperature, specific humidity, short and long-wave radiation and air pressure) measured above the canopy at the site from 2002-2004. The short-wave radiation

was split into 68% direct and 32% diffuse, and then this was split into 43% visible and 57% near-infrared for direct, and 52% visible and 48% near-infrared for diffuse (Goudriaan, 1977).

The soil properties were standardised across all models to create a similar soil physical environment. An 8 m depth soil environment with a free draining lower soil layer was implemented in all models. Similarly all models set hydraulic conductivity at field capacity to 0.1 mm day^{-1}. Calculated soil matrix potential at saturation (Ψ_s, MPa), hydraulic conductivity at saturation (K_s, m/s), and soil water content at saturation (θ_s, m^3 m^{-3}) were calculated according to Cosby et al. (1984) and volumetric soil water content (SWC m^3 m^{-3}) at field capacity (θ_{fc}), wilting point (θ_{wp}), and air dry point (θ_{ad}) according to Clapp and Hornberger (1978). Specific details of the soil equations and the effects they have on each model are discussed by Christoffersen et al. (in prep). Biological properties such as rooting depth, root biomass, as well as the total number of soil layers were left as model specific soil properties. Prior experiments have shown that these soil adaptations created a similar abiotic soil environment across all models (Christoffersen et al., in prep).

5.3.4 Experimental design

All of the models went through a standard spin-up procedure prior to all model simulations. This spin-up procedure was split into two parts. The first spin-up involved running the models from bare-ground using recycled meteorological data from 2002-2004 and pre-industrial CO_2 (278 ppm) until all of the model carbon pools reached steady state. Following this a second transient spin-up was performed,

using the same recycled met data to run the models from 1715 to 1999, over which time CO_2 was increased using measured atmospheric CO_2 from 278 ppm to 1999 values. The second spin-up period was designed to allow for any model changes in vegetation composition and structure which may result from increasing CO_2 concentrations.

Following on from this spin up period, a series of five model runs, with varying air temperatures were performed over a 8 year period (1999-2006) for ambient precipitation (control simulations) and for simulations with a 50 % reduction in wet season rainfall for 2000-2006 (drought simulations). The 2002-2004 met data was recycled from 1999-2006 to allow us to simulate an eight year run, (1999-2006), the first year of which never incurred any changes from ambient temperature and precipitation. To explore the effects of changes in air temperatures on the models we performed five model runs which consisted of runs with ambient air temperature adjusted by -5 °C, 0 °C (ambient air temperature), +2 °C, +4 °C and +6 °C, for each hour. Our analysis was focused mainly on increases in temperature; however we included a run with temperatures 5 °C lower than ambient temperatures, on the basis that some models may have processes optimised for temperate regions where average air temperatures are lower. Vapour pressure deficit (VPD) was adjusted according to the changes in air temperature. The changes in air temperature were implemented for the whole of 2000-2006 on both the modelled control and the drought simulations.

5.4 Results

To compare the models' predictions of the canopy scale flux of NEE with the flux

data collected by Doughty and Goulden (2008) we extract canopy level fluxes from wet and dry season when photosynthetically active radiation (PAR) was >1000 μmol m^{-2} s^{-1}. PAR was not available for the whole period, therefore we use the measured shortwave radiation to estimate PAR. A conversion factor of 2 is used to convert from shortwave radiation (W m^{-2}) to PAR (μmol m^{-2} s^{-1}); this factor was based on a relationship calculated from the flux tower at the study site (Doughty, unpublished data). We focus our leaf scale analysis of stomatal conductance, evapo-transpiration, and photosynthesis on periods of high PAR (>1000 μmol m^{-2} s^{-1}); however to more accurately test for the effects of both direct and indirect effects of temperature on photosynthesis we also focus the leaf level analysis on the dry season (July to December) when both air temperature and VPD are higher and soil water content is lower. The results from each model for the period of (2000-2006) for the five ambient temperature runs (with offset of -5 °C, +0 °C, +2 °C, +4 °C and +6 °C) were pooled. Model output was then placed into 1 °C bins of air temperature for the canopy-scale analysis (GPP, NEE, ecosystem respiration (R_{eco})) or leaf temperature, for leaf scale analysis (as in Doughty and Goulden 2008). Accounting for non-gaussian distributions in model output the median and the 15.9^{th} and 84.1^{th} quantiles of the binned model output are plotted to represent the mean and standard deviation of the temperature response curve of any model variable. The data from the drought and control simulations are considered separately. ED, unlike the other models, simulates sapling growth; however saplings in ED contribute very little to the canopy level fluxes of GPP. To be representative of the average leaf level responses which produce the GPP response we therefore only include trees in ED which are ≥10cm diameter in our calculations of average leaf level fluxes.

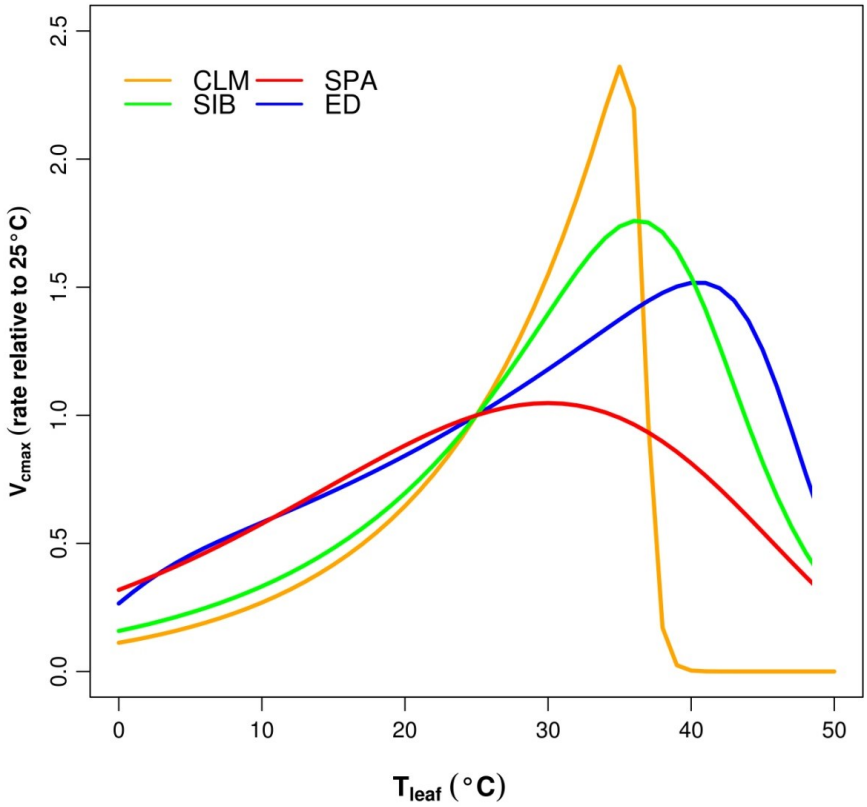

Figure 5.2: The temperature response of V_{cmax} for each model show relative to the V_{cmax} at 25 °C for CLM (orange), ED (blue), SiB (green) and SPA (red).

5.4.1 Direct and indirect leaf temperature responses on photosynthesis

All of the models can simulate a direct effect of leaf temperature on leaf photosynthesis, through a temperature optimisation of V_{cmax} and an indirect effect of temperature on leaf photosynthesis, through the effects of temperature induced changes in VPD on stomatal conductance. The optimum point of V_{cmax} for each of the models is shown in Figure 5.2. At temperatures rose above 25 °C the variability between the model responses of V_{cmax} increased (Figure 5.2). In CLM, ED, SiB and SPA the V_{cmax} optima was set to 35 °C , 40 °C, 36 °C and 30 °C respectively.

However, in SiB the V_{cmax} did not decline sharply until temperature rose above 39 °C and in SPA there was a much steadier decline in V_{cmax} with increasing temperature after the optimum point, relative to the other models.

The canopy average g_s values in ED and SiB reach substantially higher values than those of CLM and SPA (Figure 5.3a). The highest median g_s value was 807.1 mmol m^{-2} s^{-1}, at a leaf temperature of 29 °C in the ED model; in contrast the peak median value in the CLM model was 67.8 mmol m^{-2} s^{-1} at 26 °C. The effect of leaf temperature on g_s is mediated through the effects of changes in vapour pressure at the leaf surface, which is represented as VPD in Figure 5.3b. As leaf temperature rise above 25-27 °C, CLM, SiB and SPA show a similar increase in the VPD (Figure 5.3b; the data on VPD was not available from ED, although we expect the output to be similar to the other models). All of the models show declines in g_s with increasing leaf temperature and VPD (Figure 5.3a). The decline in g_s has the greatest effect on reducing evaporative loss in CLM and SPA, which demonstrate the steepest decline in leaf evapo-transpiration after 35 °C and 30 °C respectively (Figure 5.3d). CLM, ED and SiB all simulate a soil water stress factor (β). In CLM the strong constriction in E_t is caused by the effect of β on g_s (see Appendix 2 for model code). Figure 5.3e shows that in CLM there is an 87% reduction in β as leaf temperatures increase between 30-42 °C; this causes g_s to drop close to zero. The decline in β with increasing temperature in ED and SiB was only 10% and 26% respectively (Figure 5.3e). As the reduction in β is low in ED and SiB the steep decline in g_s in these models (Figure 5.3a) can only be caused by the effect of atmospheric waster stress.

The decline in net photosynthesis (A_n) in CLM, ED, SiB and SPA occurs after leaf

temperatures of 30 °C, 30 °C, 26 °C and 25 °C, in each model respectively. In all models the decline in the canopy average A_n occurs at, or within 1 °C of the leaf temperature at which g_s starts to decline (Figure 5.3a-5.3c) and significantly before the optimum point on V_{cmax} (Figure 5.2). However, in all models there is a slight increase in the rate of decline in A_n after the point at which each model reaches its optimum V_{cmax}. The rate of decline in A_n varies significantly between the models. From the model optimum point of A_n the maximum decline was in CLM (Figure 5.3c), where there was a decline of 85% in A_n. In contrast the lowest decline in A_n with increasing temperature was in SiB where there was a 48% decline. At a leaf temperature of 25 °C the range of A_n values is 1.15 μmol m^{-2} s^{-1} and this increases by 2.6 times at leaf temperatures of 42 °C where the model range of A_n values is 2.95 μmol m^{-2} s^{-1}(Figure 5.3c).

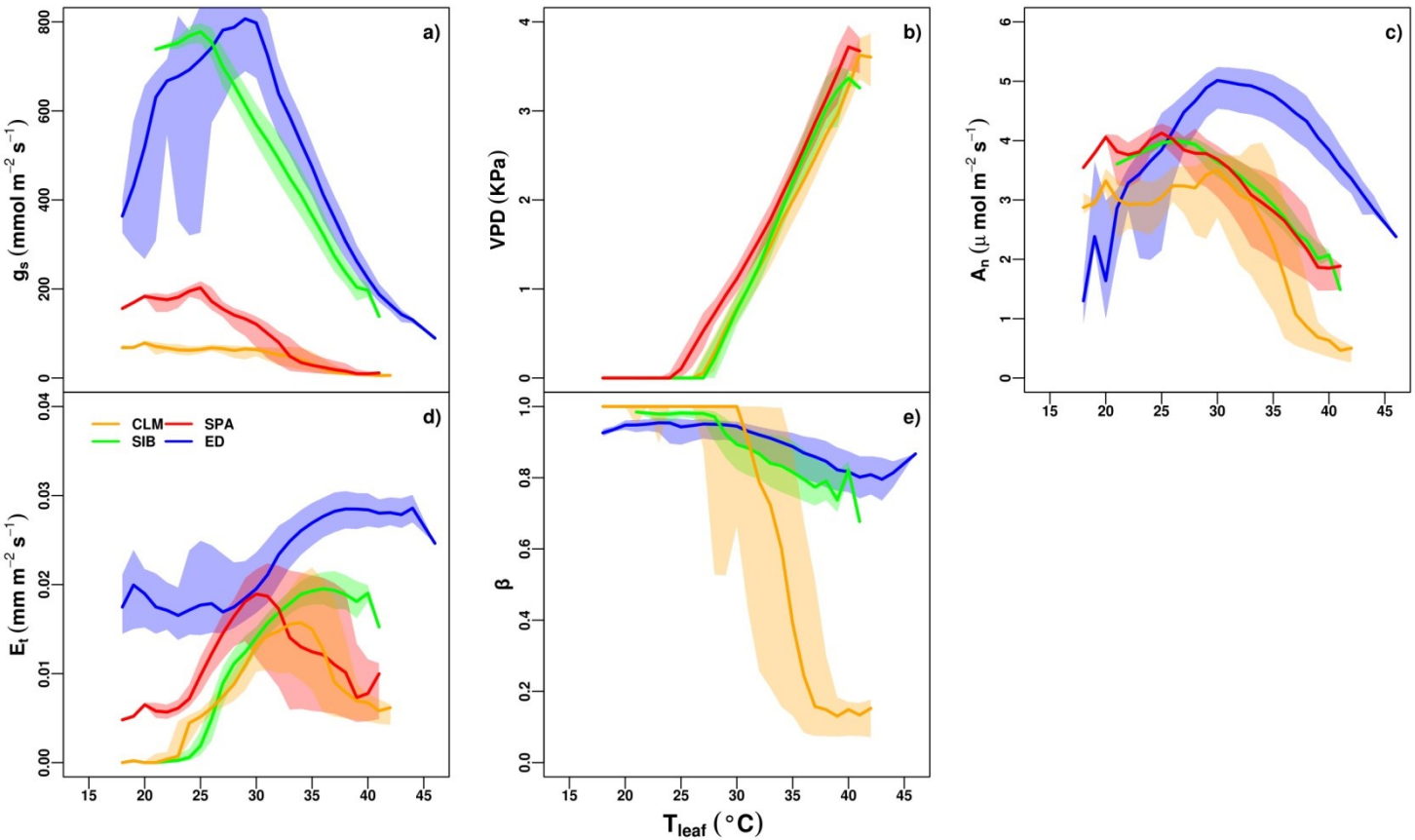

Figure 5.3: Comparison of the leaf temperature ($T_{leaf;}$ °C) response of stomatal conductance (g_s (μmol m^{-2} s^{-1}); panel a), vapour pressure deficit of canopy air (VPD (KPa); panel b), net photosynthesis (A_n (μmol m^{-2} s^{-1}); panel c), leaf evapo-transpiration (E_t (mm m^{-2} s^{-1}); Panel d) and the soil water stress factor (β; panel e) for average canopy leaves in CLM (orange), ED (blue; note data on VPD was not available from ED) , SiB (green) and SPA (red; note SPA does not simulate β). The lines show the median model responses from the control plot for the five temperature simulations (ambient air adjusted by -5 °C ,0 °C, 2 °C, 4 °C, 6 °C) pooled and divided into 1 °C temperature bins for each model. The model data is taken from the dry seasons of 2000-2006 when photosynthetically active radiation was >1000μmol m^{-2} s^{-1}. The shaded areas around each line show the 15.9th and 84.1th quantiles.

5.4.2 The effect of temperature change on the forest carbon balance

The temperature response of NEE provides important information on how the carbon balance of the site is altered by temperature. Figure 5.4a shows the response of NEE (negative value indicate uptake) measured across wet season and dry season to changes in air temperature when PAR is >1000 μmol m^{-2} s^{-1}. Doughty and Goulden (2008) observed a steep increase in NEE from -17.4±0.3 to-7.9±1.1 μmols m^{-2} s^{-1}, as ambient air temperatures rose between 28 °C - 32 °C (Figure 5.4a). SPA provides the most accurate representation of this steep increase, however the increase in NEE from SPA occurs at lower temperatures (24 °C) than observed in the data (Figure 5.4a). The increase of NEE in SiB occurs at an air temperature closer to the data (27 °C), however the rate of increase is too low in SiB, as it is in CLM and ED (Figure 5.4a). Relative to the modelled leaf scale temperature responses of g_s, A_n, E_t and V_{cmax}, the modelled NEE temperature responses show much more consistency between the models (Figure 5.2, 5.3a, 5.3c, 5.3d and 5.4a).

The decline in modelled NEE at high temperatures is caused mostly by a decline in GPP (Figure 5.4b). As air temperatures increases from 16 °C to 38 °C the average decline in GPP from all four models is 19.0±9.5 μmol m^{-2} s^{-1}. In contrast the mean model decline in R_{eco} over the same modelled air temperature range was 2.9±4.5 μmol m^{-2} s^{-1} (Figure 5.4b and 5.4c). The decline in ecosystem respiration is low because in all the models there is a decline in autotrophic respiration with increasing temperatures, which is balanced by an increase in heterotrophic respiration with increasing air temperatures (data not shown).

Between 25 °C to 38 °C the decline in GPP in CLM and SPA (91 % and 82%

respectively) was significantly greater than in ED and SIB (56 % and 44 %, respectively; Figure 5.4b). The pattern of steeper decline in GPP in CLM and SPA matches the relatively greater decline in median LAI between 25 °C to 38 °C (4.2 m^2 m^{-2} and 4.4 m^2 m^{-2} respectively) than in ED and SiB (0.6 m^2 m^{-2} and 0 m^2 m^{-2}, respectively; Figure 5.4d). The decline in LAI in SPA occurs after 25 °C; the point when VPD starts to rise and g_s and A_n start to decline (Figure 5.3a and 5.3c). Similarly in CLM after 30 °C (the point at which at which both g_s and A_n decline) LAI starts to continuously declining (Figure 5.3a and 5.3c). In SiB LAI is constant and ED only showed relatively small declines in LAI from 24 °C onwards (Figure 5.4d), before the point at which g_s and A_n decline in ED (Figure 5.3 and 5.3c). However, more notable than the decline in LAI in Figure 5.4d is the large range in the LAI values; at temperature below 25 °C ED has a median LAI of (3.8 m^2 m^{-2}) which is >3 times lower than the LAI in CLM (11.6 m^2 m^{-2}).

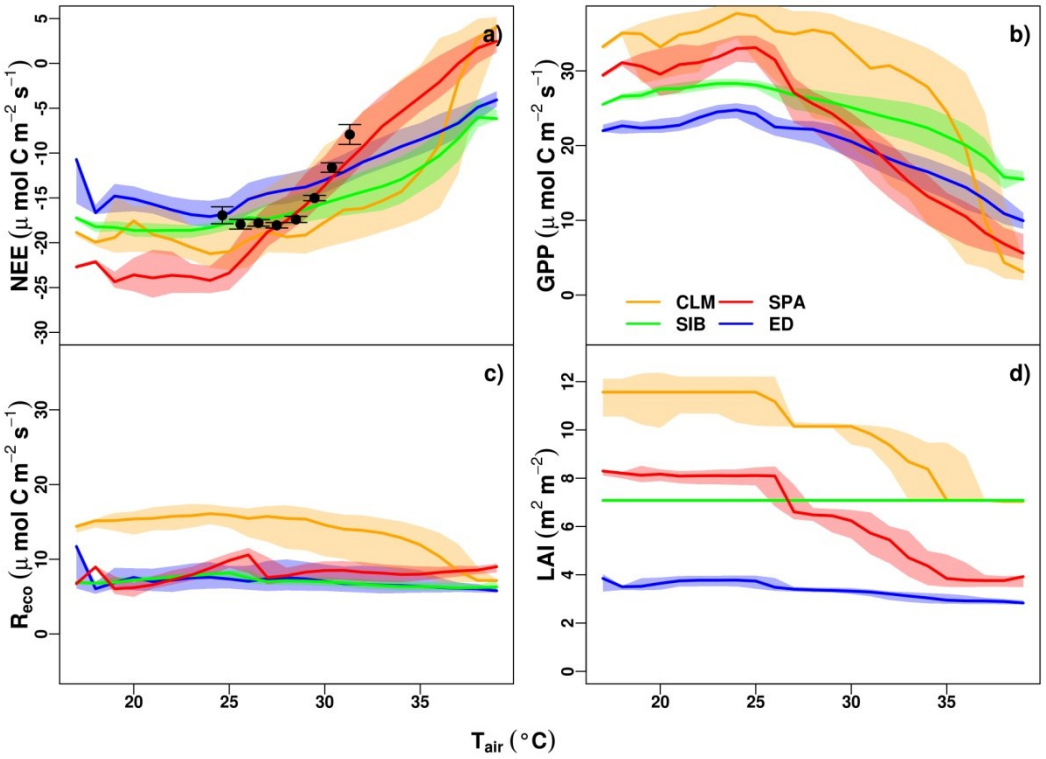

Figure 5.4: Comparison of the air temperature (T_{air} °C) response of net ecosystem exchange (NEE (μmol m^{-2} s^{-1}); panel a, note that negative values of NEE indicate carbon sequestration), gross primary productivity (GPP (μmol m^{-2} s^{-1}); panel b), ecosystem respiration (R_{eco} (μmol m^{-2} s^{-1}); panel c) and leaf area index (LAI(m^2 m^{-2}): panel d) from for CLM (orange), ED (blue), SiB (green) and SPA (red). The lines show the median model responses from the control plot for the five temperature simulations (ambient air adjusted by -5 °C ,0 °C, 2 °C, 4 °C, 6 °C) pooled and divided into 1 °C temperature bins for each model. The model data is from both wet and dry season, 2000-2006 when >1000μmol m^{-2} s^{-1}. The shaded areas around each line show the 15.9th and 84.1th quantiles. The black points and error bars in panel a) show the measured NEE from Figure 4 in Doughty and Goulden (2008).

5.4.3 The interactive effects of temperature and drought

The relative sensitivity of the four models to changes in temperature and precipitation is assessed through comparing the interactive and non-interactive effects of the 50 % reduction in wet season precipitation (drought simulation) with the -5 °C, 0, and +6 °C change in air temperature on ecosystem fluxes at the end of the 8 year simulation (2006). All of the models predict between a 10-30 % increase in GPP values and 6-10 % increase in R_{eco} when the ambient air temperature is reduced by 5 °C (Figure 5.5). The greater change in GPP than R_{eco} with the temperature reduction results in a significant increase of carbon sequestration (CLM, ED, SPA) or reduction in carbon loss (SiB; Figure 5.5).

In all models there was an interactive effect of drought and temperature on GPP, R_{eco}, NEE and excluding SiB for LAI also (Figure 5.5). This interaction was strongest in CLM where there was no change in the GPP between the control and drought simulation at ambient air temperature -5 °C, contrasting the situation at ambient air temperature +6 °C where there was a shift from a GPP value of 28 Mg C ha^{-1} yr^{-1} in the control simulation to a complete loss of forest to grassland in the drought simulation (values from the grassland environment are not plotted in Figure 5.5). Similarly in SiB and SPA there was no decline in GPP between the control and the drought simulation at air temperatures 5 °C below ambient, but a 58% and 46% respective decline in GPP in the drought compared to the control simulation at ambient air temperature +6 °C. The interactive effect of temperature and precipitation change was lowest in ED, where there was a persistently strong drought effect on GPP, and R_{eco} at all temperature levels (Figure 5.5).

For each model we assess the relative sensitivity to changes in temperature and drought through calculating the average increase in air temperature, across our simulated temperature range, which causes the equivalent change in GPP as the 50 % reduction in wet season precipitation. There was high variability in the temperature rise necessary to cause the same effect on GPP as the drought simulation at ambient temperatures. The equivalent temperature value was lowest in SPA and CLM (5 °C and 5.62 °C, respectively) and highest in SiB and ED (15.7 °C and 17.5 °C, respectively), demonstrating that SPA and CLM, relative to ED and SiB, are significantly more sensitive to temperature change than drought. CLM and SPA also show a strong feedback between LAI and GPP (Figure 5.5). ED did demonstrate a GPP, LAI feedback but this was significantly stronger with drought than temperature (Figure 5.5) and, was caused by greater mortality in the drought simulations.

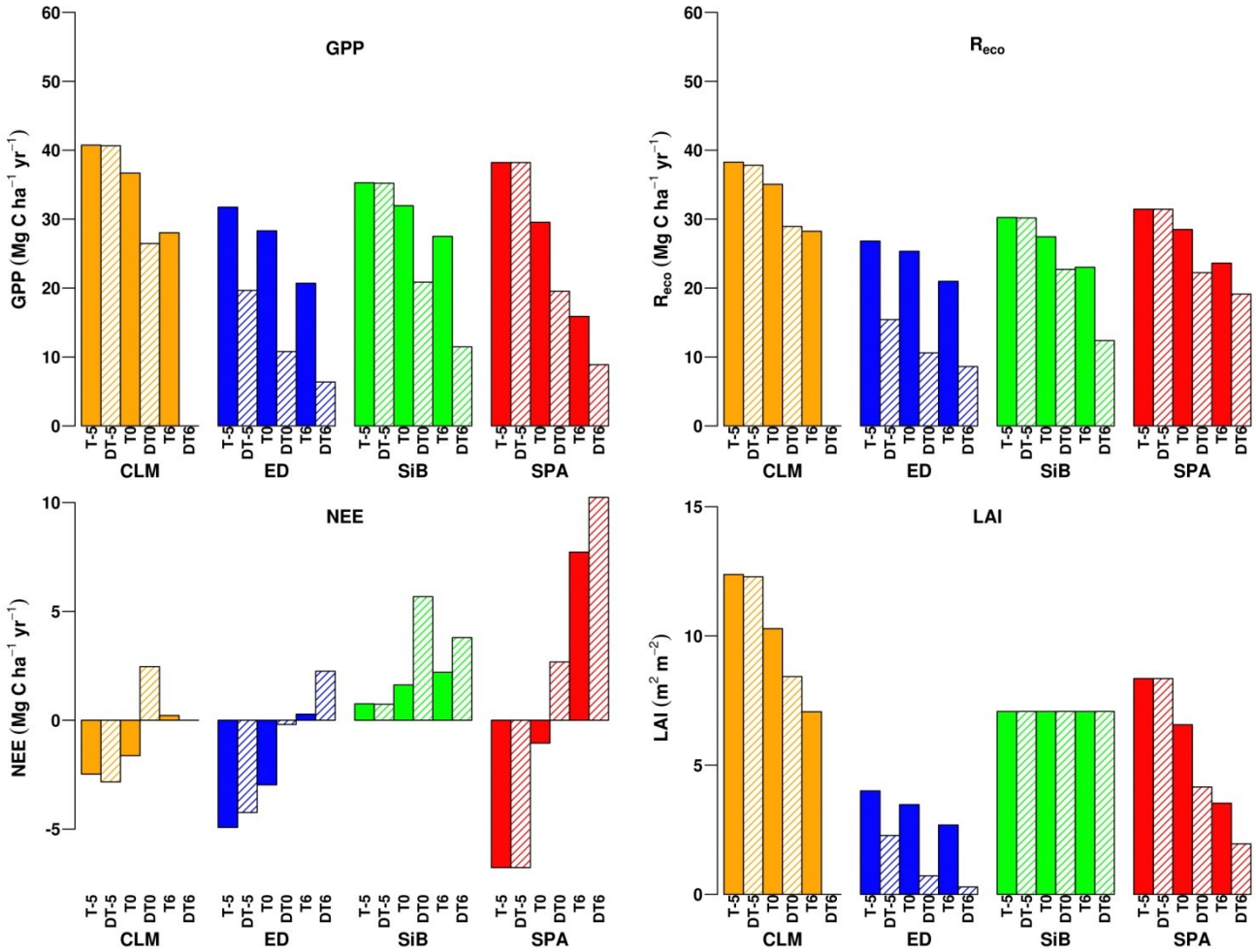

Figure 5.5: The change in the values of gross primary productivity (GPP; Mg C ha^{-1} yr^{-1}), net ecosystem exchange (NEE; Mg C ha^{-1} yr^{-1}), ecosystem respiration (R_{eco}; Mg C ha^{-1} yr^{-1}) and leaf area index (LAI; m^2 m^{-2}) at the end of the final year (2006) for the ambient air temperature -5 °C (T-5), +0 °C (T0), and +6 °C (T6), on the control plot (solid bars) and on the droughted TFE plot (indicated with a D and dashed bars), for each model (CLM: orange, ED: blue, SiB: green, SPA: red).

5.5 Discussion

This study has shown a very broad range of both the values and the temperature responses of leaf and canopy scale fluxes between the vegetation models. We have demonstrated that there is high variability in the values of physiological parameters such as V_{cmax}, and g_s, as well as structural model parameters such as LAI. Large variations in parameters such as these demonstrate that models currently have very different approaches to simulating tropical forests and thus unsurprisingly very different sensitivities to variations in atmospheric temperature and precipitation. In the following section we will discuss these issues further and highlight the necessity for further work to constrain these model responses.

5.5.1 Direct versus indirect effects of temperature change on photosynthesis

Assessing whether temperature change alters photosynthesis by either direct or indirect changes to leaf physiology is important in determining how temperature rise affects net assimilation rate, an issue which currently remains unresolved in Amazonian forests (Doughty and Goulden, 2008; Lloyd and Farquhar, 2008; Doughty, 2011). The effect of high temperatures on V_{cmax} is the only direct mechanism through which temperature can reduce leaf photosynthesis in all four models (see Appendix 2 for further details). In SPA high temperatures can also reduce J_{max}, however this temperature response is optimised to the same temperature as V_{cmax}, and has an almost identical form (data not shown). Without explicitly separating the direct and indirect effects of temperature on photosynthesis within

models (Galbraith et al 2010), it can be difficult to determine whether simulated photosynthetic limitations are caused by changes in g_s or V_{cmax}. However, any decline in A_n prior to the optimum point of V_{cmax} (Figure 5.2) can only be the result of indirect effects of g_s. In all models declines in A_n started to occur at temperature which were significantly lower than the optima point of V_{cmax} (Figure 5.2 and Figure 5.3c). The declines in A_n were therefore initiated by and followed the patterns of declines in g_s caused by increased VPD and the soil water stress (Figure 5.3a-d). Therefore it seems that H1, which suggested the models would demonstrate a greater influence of indirect controls of photosynthesis, is correct.

All of the models showed A_n to be declining at temperatures beyond 30 °C, therefore reflecting the results of leaf measurements performed by Doughty and Goulden (2008). However, instantaneously measuring the response of A_n and g_s to rising leaf temperatures, as done by Doughty and Goulden (2008), does not capture the effects of soil water restrictions on g_s and therefore A_n, which occur as higher atmospheric temperatures lead to greater evaporative losses. In CLM g_s was strongly limited by the effect of the soil water stress factor β (Figure 5.3a, and 5.3e); contrasting ED and SiB which demonstrated a greater influence of atmospheric than soil water stress on g_s (Figure 5.3a, and5.3e). The three models which use β, all have different ways of calculating β (see Appendix 2 for details), which could be the cause of such differences in the response of β to temperature; however much more likely is that differences in soil water stress are caused by significant differences in the way the models simulate plant available water and root water uptake, which has been demonstrated by Christofferson et al., (in prep), when simulating the Tapajós site with these models. Previous studies have shown that in Amazonian tropical forests

restrictions in A_n and g_s is caused when reductions in soil water availability prevent the tropical trees meeting atmospheric demand for water (Nepstad et al., 2002; Fisher et al., 2006; Fisher et al., 2007). Therefore we reject H2, which suggested that g_s would be restricted by soil water stress finding no consensus as to whether soil or atmospheric water stress provides the greatest limitation on g_s in models. It seems therefore that to resolve the variability in the impact of water stress on g_s in CLM, ED and SiB it is necessary for models to simulate the interactive effects of atmospheric demand and belowground supply of water. The SPA model, which currently simulates such hydrodynamics, has been shown to be more accurate at simulating root water uptake and the effects of soil water reductions on sap-flow and evapo-transpiration in tropical forests (Fisher et al., 2007; Christoffersen et al., in prep).

Despite similarities in the direction of the responses of photosynthesis across the models, there was high variability in the sensitivity of g_s, E_t, A_n and V_{cmax} to temperature change between the models. For example, the model range for canopy average g_s values at a leaf temperature of 25 °C was 64.1-715.5 mmol m^{-2} s^{-1}. Such high variability in the values of an average canopy leaf between the models is a cause of concern and suggests that a detailed evaluation of how accurately these models reflect measured tropical leaf physiology is of great importance.

5.5.2 The effect of changes in temperature on the carbon balance.

Despite the high variability in the leaf level responses, all of the models simulate NEE values which are closely aligned to values measured at our study site (Figure

5.4a). Across all the models, as we hypothesised (H3) the NEE response to temperature is driven by the relatively greater sensitivity to temperature of GPP than R_{eco} at high light levels (Figure 5.4b and 5.4c). The temperature response of GPP in SiB, the model with the simplest canopy structure, closely mimics the response of A_n to leaf temperature (Figure 5.3c and 5.4b). This may reflect the loss of detail in simple canopy models relative to models with more complex light interception schemes, which simulate the diversity of radiation within tropical forest canopies (Williams et al., 1998; Mercado et al., 2006; Mercado et al., 2009). The similarity in the response of GPP and A_n to temperature may however, also reflect the lack of interaction between LAI and GPP in SiB, in contrast to the other models. The steep decline in both GPP and LAI in CLM and SPA (Figure 5.4b) reflects the feedback in which reduction in A_n causes reductions in LAI and therefore lower GPP. In ED the connection between GPP and LAI differs from CLM and SPA because ED is the only model which simulates the mortality of individual trees (see Medvigy et al., 2009 for further details), which appears to increase very little with increasing temperature. We accept H4 finding that, where present, the effect of structural changes in LAI cause important feedbacks on GPP. Given the importance of leaf area when scaling from the leaf to the canopy in these models, we suggest accounting for canopy structural feedbacks when predicting the sensitivity of tropical forests to changes in temperature and drought is necessary. However this is of course only of value if both the canopy and the leaf level values are accurately represented. Therefore the range of LAI values and responses presented in this study (Figure 5.4d) is something which needs to be urgently addressed.

5.5.3 Combined drought and temperature sensitivities

Across the four models, as hypothesised (H5), we demonstrate that, at the canopy scale, all the models show negative responses of GPP to rising air temperature and an amplification of the negative effects of temperature with drought (Figure 5.5). Interestingly we demonstrate that all of the models simulate an increase in GPP of between 3.3-8.7 Mg C ha^{-1} yr^{-1} if ambient air temperature is reduced by 5 °C (Figure 5.5). This result demonstrates that these models diagnose that the simulated forest is operating at a temperature and VPD levels beyond its optimum. At multiple sites across the globe, including the Tapajós site, Lou et al (2008) tested how sensitive ecosystem respiration and net ecosystem productivity was to changes in multiple climatic variables including, temperature and drought in four vegetation models. Like Lou et al. (2008) we find that the sensitivities of these models to changes in temperature and, simultaneous change in drought and temperature show notable differences. However in this study we go further than Lou et al., (2008) and explore the processes underlying such differences in greater detail. All the models demonstrated greater negative effects on ecosystem fluxes and LAI if the drought was combined with increases in air temperature above ambient levels; however the strength of this impact varied greatly between models (Figure 5.5).

Both CLM and SPA showed the strongest temperature responses on GPP, R_{eco} and LAI: SiB had a similar magnitude drought response to CLM and SPA but a much weaker temperature response. Interestingly however, the interactive effect of temperature rise and drought was strong in SiB, demonstrating that the rising air temperature only had a very strong effect in drought conditions (Figure 5.5). In contrast in ED the drought effect on GPP is significantly stronger than for the other

models because of a strong mortality effect in drought conditions at this site (Figure 5.4a; also see Powell et al., in prep). The range of temperature increases, across our simulated range, to reproduce the equivalent effect of a 50 % reduction in wet season rainfall across the models was therefore very large (5-17.5 °C). Previous modelling studies have shown that there is high variability in how sensitive models are to temperature and drought (Friedlingstein et al., 2006; Luo et al., 2008; Sitch et al., 2008; Galbraith et al., 2010), but that vegetation model seem to have greater sensitivity to rises in temperature than drought (Galbraith et al., 2010). Our results paint a slightly more complex picture, in that although we find high variability in the sensitivity of models to drought and temperature, we find that some models appear to have low temperature and high drought sensitivity and others vice versa. As a 6 °C rise in temperature and a 50 % reduction in rainfall are possible changes which may occur in Amazonia during the 21st century (Christensen et al, 2007) we reject H6, which suggested that models will simulate a stronger temperature than drought response, as we find no consensus between vegetation models as to whether they will predict stronger drought or temperature effects under scenarios of future climate change.

5.6 Conclusion

The question of precisely how tropical forests will responds to warming temperatures and reductions in precipitation is yet to be resolved. Using four sophisticated vegetation models we find that at a canopy scale all of the models simulate a negative response to air temperatures rising above ambient levels, and this effect is

amplified to some degree in all models by a simultaneous 50 % reduction in wet season rainfall. We find that at leaf scales the models do not simulate strong direct effects of temperature on A_n; instead all the models showed strong initial declines in A_n caused by indirect effects of temperature on A_n via the effects of VPD and soil water stress on stomatal conductance. The model variability in the sensitivity of leaf level fluxes to changes in leaf temperature/VPD, particularly g_s, is significantly greater than the model variability in the sensitivity of NEE (canopy scale) to air temperature. The magnitude of the feedback between A_n, LAI and GPP was important for determining how models responded to temperature and drought, as was the feedback between E_t, soil water stress and g_s.

The sensitivity of the models to changes in temperature and precipitation varied widely between the models. The average rise in temperature to cause the same average reduction in GPP as the simulated drought varied between models by 5-17.5 °C. Over the ranges of temperature and precipitation change explored in this study, we find no consensus between the models as to whether vegetation models can be considered more sensitive to change in drought or precipitation in Amazonian forests. The degree of model variability we demonstrate has significant consequences for our current capability for predicting the effects of future climate change on Amazonian forests. We suggest that if indeed indirect photosynthetic responses to rising temperature are the primary limitation in these forests, something which still needs greater empirical testing, models need to accurately simulate the connection between atmospheric demand and below ground supply of water to accurately represent the stomatal responses to temperature. Secondly we suggest that models need to correctly simulate the feedback between leaf area and GPP to accurately

represent temperature and drought responses; however prior to this models must first accurately simulate LAI. Lastly we suggest that testing leaf scale, as well as canopy scale responses must be part of model testing protocols and that the leaf temperature responses in vegetation models need to be more rigorously tested against empirical data, which itself needs to be targeted at understanding the sensitivity of tropical leaves to long term warming and the associated soil water depletion.

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Chapter 6: Discussion

6.1 Thesis Overview

The aim of this thesis was to reduce the uncertainty associated with predicting how sensitive Amazonian forests are to changes in climate. I have used a variety of data sources, and novel analytical techniques to target three key areas which I identified in the introduction (Figure 1.2): uncertainty associated with ecological processes; uncertainty associated with how models are parameterised; and uncertainty associated with differences in model structure. I believe that this PhD provides new insights these areas, and therefore to how climate change may affect the forests of Amazonia. In this chapter I summarise my key findings and discuss how they contribute to reducing the uncertainty in the three key areas identified in Figure 1.2 and to the wider goal of predicting the effects of climate change in Amazonian forests. Finally I also discuss further research ideas which have arisen from the research performed in each chapter.

6.2 Key findings from Chapter 2 regarding the sensitivity of wood production to changes in climate

In this chapter I reported the comprehensive assessment of the effect of seasonal changes in climate on the woody productivity using the longest dataset available for tropical forests, from two forest plots in western Amazonia. The chapter details the sensitivity of woody productivity to seasonal changes in climate and the potential utility of using a functional traits framework as a tool for modelling the sensitivity of

woody production to changes in climate. The key findings of this chapter were:

1. On the two study plots I found a reduction of wood production of between 40 and 60 % in peak dry season relative to peak wet season. This reduction closely followed reductions in precipitation, soil water content and increases in water deficit in this forest.
2. I found that anomalies of stem productivity, which I used to test for evidence of interannual variability, significantly correlated with anomalies of SWC ($r^2=0.49$, $p=<0.01$), but only on the one forest plot where there was a clay soil and a greater abundance of low wood density trees.
3. The relative strength of seasonal changes in growth rate between trees was related to functional traits. Annual stem growth rate, tree height and tree diameter were positively related to stronger seasonal growth patterns, whilst wood density was negatively related to seasonal growth patterns. This result is consistent with a hypothesised trade-off between maximum potential growth and hydraulic safety.

6.2.1 Implications for predicting future change in the Amazon

This is the first study to comprehensibly assess, over a five year time series, the effects of seasonal changes in climate on wood productivity and provides a robust set of results which accounts for the effects of interannual variability. The correlation between seasonal anomalies of wood productivity and SWC suggests that these forests are already sensitive to lower than average soil water contents. I found no correlation between wood productivity and interannual anomalies of air temperature, finding no support for the hypotheses which suggest Amazonian forests are already

operating at, or above their temperature threshold (Clark et al., 2003; Feeley et al., 2007). The connection between the sensitivity of trees to dry season reduction in soil water and functional traits, suggests that models which incorporate functional traits (Fyllas et al., 2012) may provide a more accurate representation of the sensitivity of these forests to future change. The analytical power a long term, seasonal time-series of dendrometer measurements on more than 1200 tropical trees has, provided a new insight into the seasonality of woody productivity which has reduced uncertainty concerning the measured process, and provided information which could be used to parameterise the differences in the vulnerability of trees from different functional groups to water stress within vegetation models. Consequently this chapter has directly targeted the goal of reducing the uncertainty related to key ecological processes involved in understanding climate change in the Amazon, and provided new information which could be used to reduce uncertainty associated with model parameterisation.

6.2.2 Ideas for progression of the research in chapter 2:

1. This study indicated that there were differences in the seasonal responses between two forest plots. This may be related to the differences in the distribution of the functional traits between the two plots or to variations in soil properties. Other studies in the Amazon have found that soil properties and variations in forest composition are an important determinant of patterns of woody biomass stocks (Malhi et al., 2006; Baraloto and Couteron, 2010; Quesada et al., 2012). Dendrometer studies are ongoing at many permanent plots which are part of the RAINFOR network (http://www.rainfor.org/). Although the existence of seasonal dendrometer data over long periods is

rare, ongoing research will provide the potential to study how the climate sensitivity of woody productivity varies between forests on different soils and with different floristic composition. Such data will give a valuable insight into the wider relevance of soils and/or functional traits on influencing the vulnerability of different forests to changes in soil water content across Amazonia.

2. The finding that functional traits are linked to the vulnerability of certainty trees to water availability is a topic that could easily be explored using modelling studies. Fyllas et al. (2012), have already demonstrated the potential for incorporating functional traits into modelling studies and, further studies are already planned to test the capacity of models incorporate functional trade-offs in tropical forests and to collect further data to inform how this can be linked to drought vulnerability (U.S.DOE., 2012)

6.3 Key findings from Chapter 3 regarding the sensitivity of respiration from coarse woody debris to changes in precipitation

In this study at the Paracou tropical forests site in French Guiana I presented the first analysis of the sensitivity of respiration from tropical dead wood to seasonal changes in climate and the relative importance of biotic and abiotic factors for modelling this sensitivity. The key findings of this chapter were:

1. There was a significant seasonal change in the respiration rates of coarse woody debris (R_{cwd}); mean R_{cwd} dropped by 35.6±5.1 % from wet to peak dry

season.

2. There was a significant positive correlation between R_{cwd} and the woody tissue moisture of the coarse woody debris (CWD) samples, suggesting that the decomposers inside the CWD samples responded negatively to reductions in available moisture. The strength of the correlation between woody tissue moisture and R_{cwd} rate of samples was, however strongly related to the initial wet season moisture status of the CWD.
3. Soil water content explained 60 % of the seasonal variation in R_{cwd} and can be used as a scalar to model seasonal changes in R_{cwd}.

6.3.1 Implications for predicting future change in the Amazon

CWD is poorly researched in the tropics (Chambers et al., 2001), and consequently is not normally simulated by vegetation models. Although I find R_{cwd} currently only represents a small fraction of total ecosystem respiration (5.1±0.9 %), if mortality rates increase, as has been predicted by many modelling studies of Amazonian forest (Cox et al., 2008; Harris et al., 2008; Huntingford et al., 2008) the large potential increase in CWD (up to 20-30 % loss in above ground biomass; Nepstad et al., 2007, da Costa et al., 2010) could mean R_{cwd} becomes a substantial part of total respiration, and should be included in future model frameworks. I demonstrate that the respiration in CWD has a distinct seasonal pattern in its intensity and is sensitive to changes in climate; I provide information which can be used to develop the simulation of CWD in models. Consequently this chapter has directly addressed the first goal of my thesis by providing new information about the sensitivity of an under-studied process in Amazonian forests to changes in temperature and water availability. This chapter has also provided information which can be used to develop

the structure of vegetation models to include a separate CWD pool. To effectively insert a CWD pool into models, a series of steps is needed: firstly we have to develop an effective model of tree mortality to determine rates of input into the CWD pool; secondly we need to effectively model decomposition to determine the rates of mass loss from the CWD pool, which as necessitates a knowledge of the distribution of wood density and size classes of the dying trees (Herault et al., 2010); lastly we need to use data from respiration studies such as these to model respiration rates in relation using abiotic metrics such as SWC or alternatively research new ways to link seasonal changes in respiration rates to seasonal changes in decomposition rates of CWD. Predicted increases in drought and tree mortality with future changes in climate (Cox et al., 2008) makes developing an effective model of carbon loss through the CWD pool of great importance for accurately predicting future changes in the carbon balance of Amazonian forests.

6.3.2 Ideas for progression of the research in chapter 3:

1. One of the largest uncertainties in this chapter was evident in scaling respiration measurements to a plot scale. Estimating the mass of CWD is notoriously difficult and associated with high levels of landscape variability (Clark et al., 2002; Keller et al., 2004; Chao et al., 2009). Consequently large areas need to be surveyed to account for this variability. As part of my research in French Guiana pilot surveys of the CWD volume were started on a 6.25 ha permanent sample plot. In collaboration with the ECOFOG research group (http://www.ecofog.gf/). I helped design a protocol to survey six, 6.25 ha permanent forest plots. The aims of this protocol were to determine the total volume of standing and fallen CWD, and the volume of CWD which

was derived from branch-fall events. The plots were distributed across terra firme, seasonally flooded and white sand forests, and therefore provided an excellent opportunity to explore how CWD volume and respiration varies with different environmental conditions. Currently these surveys have not been completed, but they offer a good future research opportunity.

2. In this chapter I was unable to demonstrate a temperature response in R_{cwd} because the temperature variation in the current climate at our study plot was small. However, research on R_{cwd} in other biomes has found temperature to be an important controlling factor for R_{cwd} (Jomura et al., 2007; Forrester et al., 2012). In the context of predicted future increases in temperature (Malhi et al., 2009; Marengo et al., 2012), it will be important to understand both the temperature and moisture responses on the respiration rates from R_{cwd}. It would therefore be of great interest to do warming experiments on samples of CWD, to further test for a temperature response. This study would however require significant resource and may be more appropriately done under lab conditions.
3. Quantifying the effect of the decomposer community on R_{cwd} was beyond the scope of this study. However during this study I found evidence that termites were likely to be having a significant effect on R_{cwd} (Appendix 1); although I was unable to quantify the respiratory impact of these termites during this research. Termites have been found to contribute substantially to ecosystem respiration in tropical biomes, and to the terrestrial carbon cycle via methane release (Cornwell et al., 2009). Following this study I believe that termites have a substantial impact on R_{cwd} and potentially at larger scale in this forest and I believe that determining more quantitatively the impacts of termites on tropical forest respiration is an important area of research.

6.4 Key findings from Chapter 4 regarding the impacts of seasonal drying on tropical forest carbon storage and carbon use efficiency.

In this chapter I collated all available ecological data at a tropical forest site in French Guiana for an 11 year study period. I used these datasets in a data assimilation analysis which was targeted at investigating the key processes which cause the carbon balance of this forest to change with seasonal changes in climate. The data assimilation approach allowed me to assess parameter uncertainty within a model and how this affects the certainty with which I can attribute seasonal changes in the carbon balance of this forest to changes in particular ecological processes and fluxes. The key findings from this chapter were:

1. Heterotrophic respiration (Rh) was observed to decrease by 36.0±1.4 %, in the dry season, in this forest; my analysis indicated that the dry season reduction in R_{eco} was entirely attributable to the reduction in heterotrophic respiration.
2. The rate at which this forest sequesters carbon is four times greater in the dry season than in the wet season and this change is equally attributable to an increase in GPP and a decrease in heterotrophic respiration in the dry season.
3. There was significant seasonal variation in the allocation of carbon to wood and foliage in this forest but little seasonal variation in sources of autotrophic respiration. I demonstrate that a 4.6±0.1 % increase in autotrophic respiration in the dry season partially offsets the dry season increase in GPP and results in a relatively constant carbon use efficiency of 0.35±0.02 in the wet season

and 0.37±0.02 in the dry season.

6.4.1 Implications for predicting future change in the Amazon

Seasonal changes in the flux of ecosystem respiration were greater than the seasonal change in GPP in this forest. Previous studies have detailed strong moisture responses in the respiration from tropical soils (Sotta et al., 2004; Sotta et al., 2007; Bonal et al., 2008; Meir et al., 2008) and this study demonstrates that simulating this process in models is vital for correctly simulating the carbon balance of this forest. Many modelling studies have focused on correctly simulating the response of the gross primary production (GPP) to changes in climate in tropical forests (Fisher et al., 2007; Saleska et al., 2007; Grant et al., 2009; Kim et al., 2012). However, I demonstrate that if the effect of soil water content on heterotrophic respiration had not been simulated in this study, the results would have suggested that this forest was a greater source of carbon in the dry season due to the effects of the temperature response on ecosystem respiration. Similarly I demonstrate that seasonal variability in the parameterisation of this model was important for correctly simulating the seasonal responses of ecological processes in this forest. Therefore it seems that to accurately capture the responses of Amazonian forests to climate, models need to be able to simulate the seasonal differences in allocation, turnover and respiration from different carbon pools, possibly through changing or modulating parameters with climate variables. In this chapter I have directly quantified the parameter uncertainty within a carbon cycle model, which therefore enabled me to attribute, with estimates of uncertainty, the relative contribution of different ecosystem fluxes to the seasonal changes in the carbon budget of this forest.

6.4.2 Ideas for progression of the research in chapter 4:

1. In this chapter I demonstrate the necessity to collect more data regarding the seasonal responses of root dynamics. Previous work has demonstrated that root growth and fluxes are highly spatially heterogeneous in forests (Metcalfe et al., 2007). To constraint more tightly the fluxes in this forest a comprehensive network of root measurements is necessary to better-quantify the contribution of below ground autotrophic fluxes to the total carbon balance of this forest.
2. The research in this chapter was restricted to the use of a single model, which as I demonstrated in chapter 5 may introduce bias to the simulated sensitivity of this forest to changes in available soil water and air temperature. To comprehensively understand the effects of seasonal change on the carbon balance of this tropical forest it would be interesting to implement the soil moisture response and the predicted seasonal responses of the patterns of allocation and respiration in other vegetation models.
3. I have demonstrated that this forest demonstrates significant differences in its carbon balance between wet and dry season. The logical next step would be to test how sensitive the seasonal parameterisation of this forest would be to various scenarios of future climate which could include longer dry seasons, higher temperatures, and lower rainfall higher CO_2 and lower atmospheric humidity.

6.5 Key findings from Chapter 5 regarding a model inter-comparison to explore the temperature sensitivity of a tropical forest experiencing drought.

In this chapter I used simulations from the CLM3.5, ED2 SiB3 and SPA2 models to explore how sensitive a forest in the eastern Amazon was to temperature change under drought and non-drought conditions. I reported the inter-model uncertainty on how sensitive net photosynthesis and stomatal conductance are to changes in temperature and precipitation and how this is linked to changes in ecosystem fluxes under the same conditions. The key findings were:

1. All the models simulated a stronger indirect than direct response of net photosynthesis to increases in air temperature via the effect of changes in stomatal conductance However in some models the decrease in stomatal conductance at higher temperatures was driven by soil water stress, associated with higher evapo-transpiration and in other models this was caused by higher atmospheric water stress.
2. At a canopy level, all of the models simulated the same directional response to rising temperatures and reduced precipitation. However, between the models the range of temperature increases which had the same impact on GPP as a 50 % reduction in wet season precipitation was large (5-17.5 °C), demonstrating high inter-model variability in how sensitive models were to either changes in precipitation or temperature. Some of models demonstrated a greater sensitivity to precipitation change than temperature and vice versa.
3. I demonstrate that despite high variability in the temperature sensitivity of stomatal conductance and net photosynthesis, the models seem to show much

less variability in the temperature response of NEE. Differences to model canopy structure and the feedback between LAI and GPP was important in determining such variations.

6.5.1 Implications for predicting future change in the Amazon

Previous studies have demonstrated high variability in the sensitivity of vegetation models to simultaneous changes in precipitation and drought in Amazonian forests (Luo et al., 2008; Sitch et al., 2008; Galbraith et al., 2010). In this chapter I also report high inter-model variability; however unlike previous studies (Galbraith et al., 2010), I find a variation in whether these vegetation models are more sensitive to changes in precipitation or drought. Variations in canopy structure caused important differences to the capability of models to accurately simulate the response of tropical forests to climate (Mercado et al., 2006; Mercado et al., 2009; Bonan et al., 2012). I suggest that variations in canopy structure and the feedback between LAI and GPP cause differences in the relative sensitivities of models to drought and temperature. The degree of variability between the models was large at both the leaf and the canopy scale, suggesting that currently there is high inter-model uncertainty regarding how sensitive Amazonian forests are to changes in temperature and precipitation. This uncertainty will be caused by a combination of parameter and model structural differences and this chapter therefore highlights the need to investigate and constrain these uncertainties further.

6.5.2 Ideas for progression of the research in chapter 5:

1. Chapter five represents the current findings of a much larger body of research, from which 6 peer reviewed papers will be published. Chapter five is my contribution to the second phase of this body of research, a large model inter-comparison project which set out to investigate how well current vegetation models are able to simulate the effects of a two drought experiments implemented in recent years in the eastern Amazon (Christoffersen et al., in prep; Powell et al., in, prep). The phase of this project where I contributed was concerned with testing how the drought responses in these models interacted with changes in air temperature and specific humidity. The initial phase of my analysis has been concerned with four of the six vegetation model which took part in the model inter-comparison (CLM3.5, ED2, IBIS JULES, SiB3 and SPA2). By May 2013 I hope to have received and incorporated the results from the remaining two models, JULES and IBIS, into my current analysis.
2. The key outcome of the research thus far is the dichotomy between higher temperature sensitivity in some models and higher drought sensitivity in other models. I believe that a second analysis which investigates the diurnal responses of the models at the different simulated air temperature would enable a better understanding of the relative impact of the effects of temperature on photosynthesis and how this is related to variations in canopy level fluxes of evapo-transpiration at different times of day.

6.6 Concluding remarks

Amazonian forests are of significant global value and quantifying the effect of future changes in climate on these forests is of great importance. Significant progress has been made since the first predictions of Amazon 'dieback' over a decade ago. There has been a concerted effort to improve the knowledge of the responses of ecological processes in Amazonian forests to, amongst other climatic variables, changes in temperature, and precipitation, and to quantify the uncertainties associated with simulating these in models. In this thesis I have contributed to reducing such uncertainties explicitly through improving understanding of two poorly studied ecological processes, as well as providing enhanced knowledge of the implications of parameter on inter-model uncertainty on climate change predictions. Much further work is however needed. In particular greater clarity is required regarding how respiratory processes respond to changes in climate in Amazonian forests and how this can be simulated in more detail in vegetation models. Similarly a concerted effort is needed not only to quantify more precisely the causes of inter-model variability between vegetation models, but to use this knowledge to target fieldwork at poorly understood processes. Such targeted research can then be used to provide better model constraint, and accelerate the pace at which scientists are able to understand the processes involved in climate vegetation feedbacks in Amazonian forests.

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Chapter 7: (Appendix 1) Assessing the influence of termites on the respiration rate of coarse woody debris

7.1 Overview

Termites are have a significant impact on Amazon wood decomposition (Palin et al., 2011), releasing 1.9 Pg C yr^{-1} to the atmosphere from tropical regions (Cornwell et al., 2009). In some Amazon forests termites have been found to be responsible for 20% of annual CWD decomposition (Martius, 1997). Assessment of the effect of termite respiration on respiration from CWD (R_{cwd}) is therefore important.

Termites directly break down CWD, and fragment CWD which increases the surface area to volume ratio, considerably speeding up the decay process (Harmon et al., 1986; Martius, 1997; Torres and Gonzalez, 2005; Cornwell et al., 2009; Jamali et al., 2011). Quantifying the impact of termites on the respiration rate of coarse woody debris (CWD) is hard because inter and intra-specific respiration rates of termites in the tropics are highly variable and poorly understood (Förster et al., 2006; Jamali et al., 2011). In the absence of being able to directly quantify the effects of termite activity on CWD respiration we used an index as a means to assess the degree of termite attack each sample of CWD had been subject to.

7.2 Termite Index

A termite index was given to each sample of CWD discussed in Chapter 3 to indicate the degree of termite attack the CWD was undergoing. For each of the 13 campaigns for the CWD study, the presence or absence of termites on the CWD was noted on the visible surfaces. Also a section was cut from the CWD after the final campaign, the presence of termites inside the CWD and the evidence of termite penetration into the CWD were recorded. Neither factor alone was deemed sufficient to classify termite activity due to the sporadic nature with which termites enter, leave and return to CWD over time as well as the variation in how many termites are present and how far they penetrate the CWD. Hence both metrics were used to create the following index:

0 no termites seen;

1 1 or 2 termites sporadically seen with little evidence of penetrating attack into CWD;

2 3-10 termites seen repeatedly on external CWD and/or some evidence of penetration in to outer CWD;

3 many seen repeatedly only outside of CWD and/or evidence of penetration beyond outer CWD;

4 evidence of extensive penetration by termites into the CWD;

5 CWD is densely populated with termites when cut and completely penetrated

by termites

31 out of the 42 samples of CWD in this study showed evidence of termite attack. We find that termites have effects on both the magnitude and non seasonal variability of R_{cwd} per sample (Figure 7.1 & 7.2). CWD samples with higher termite indices had higher mean respiration rates (r^2=184, p=<0.004 Figure 7.1). Although this relationship was weak its significance suggests that higher respiration rates from CWD is likely to be linked to greater termite activity.

To assess the impact of termites on the seasonal variability of R_{cwd} across the 13 campaigns, we de-trended the seasonal pattern of R_{cwd} from each sample by subtracting the moving average of R_{cwd} across all measurements periods from the absolute measured values of R_{cwd}. The standard deviation of the de-trended data represented the non-seasonal variability in R_{cwd}. The standard deviation of the de-trended data was positively correlated with the termite index for each CWD sample (r^2=0.181, p=<0.004; Figure 7.2). Although this relationship was also weak its significance suggests that termites are likely to be responsible for some of the variability in R_{cwd} that is not linked to seasonal changes in climate.

7.3 Conclusion

We conclude that termites seem to affect the magnitude, as well as the a-seasonal variability in R_{cwd}. The complexity and variability of the activity of different termite species observed during this study (Förster et al., 2006; Jamali et al., 2011), the precise numbers of which we never managed to determine, combined with the

difficulty of determining the precise degree of termite activity, makes precisely quantifying the impacts of termites on R_{cwd} very difficult. We therefore suspect that the impact of termite activity on R_{cwd} in this forest is likely to be larger than we are able to detect using coarse estimation criteria such as a termite index. Whether or not the activity of termites contributed or detracted from the seasonal patterns observed in R_{cwd} is also difficult to determine. Despite the effects of termites we still find a significant relationship between soil water content and seasonal patterns of R_{cwd}. However, it is important to note that variations in the influence of termites between different forest areas are likely to alter the relationship between SWC and R_{cwd}.

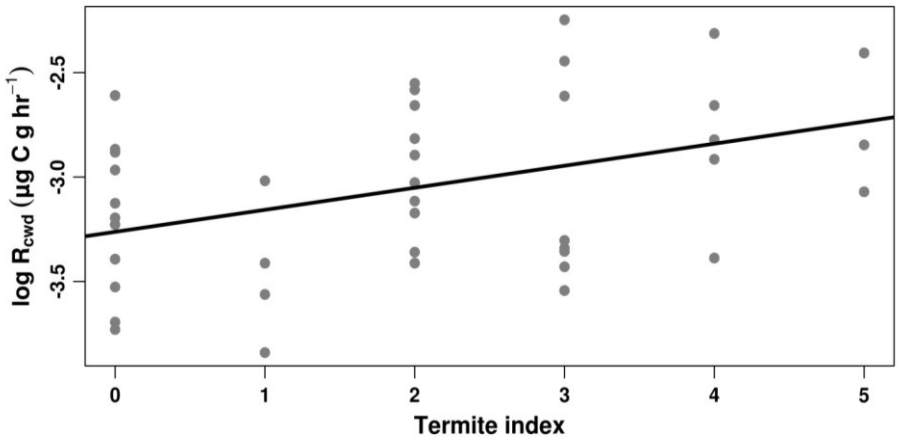

Figure 7.1: Linear relationships between log_{10} sample R_{cwd} (µg C g hr^{-1}) and termite index, (r^2= 0.184, p=0.004, top panel)

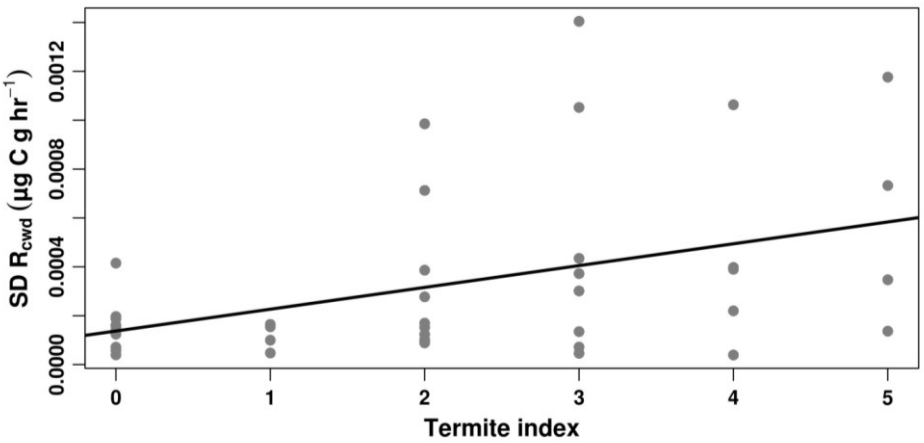

Figure 7.2: The standard deviation of the de-trended R_{cwd} data and the termite index per sample (r^2=0.181, p=0.004, lower panel).

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Chapter 8: (Appendix 2) – Model canopy structure and, the temperature and moisture response functions for each model

8.1 Model Canopy Structures:

Below the differences in the canopy structure of the five models is outlined. The models are described in order of complexity starting with the simplest.

8.1.1 SiB

The canopy in SiB is a single 'big leaf', which is not split into sunlit or shaded leaf fractions. Calculations of canopy of photosynthesis and stomatal conductance are performed at the top of the canopy and integrated over the whole canopy using a profile of leaf nitrogen and V_{cmax} calculated following a time average of the photosynthetic active radiation flux through the canopy (see Sellars et al., 1992 for further details). SiB is a diagnostic model that has a prescribed LAI which was set to 7.08 $m^2 m^{-2}$; LAI is distributed through the canopy according to a relationship to the canopy light attenuation and a spherical leaf angel is assumed for the leaf distribution (Sellers et al., 1992).

8.1.2 CLM

CLM integrates canopy calculations over a single canopy layer like SiB, but splits the canopy into sunlit and shaded leaf fractions. Sunlit and shaded leaf fractions are determined using an exponential light extinction coefficient which varies with solar zenith angle and leaf angle distribution (Dai et al., 2004). The model assumes a linear relationship between specific leaf area (SLA; m^2 g C) and height within the canopy layer; assuming therefore that SLA increases linearly with height from a fixed top canopy SLA (Thornton and Zimmermann, 2007). The values of SLA are used to determine the nitrogen per leaf area based on a fixed ratio between leaf carbon and nitrogen:

$$N_a = 1/SLA \cdot CN_L \qquad \textit{Equation 1}$$

Where N_a is nitrogen per unit leaf area (g N m^{-2}) and CN_L is leaf carbon to nitrogen ratio which is fixed for each plant functional type. Changes in nitrogen per leaf area are then used to alter V_{cmax} and therefore photosynthesis. At each time step a separate mean canopy value for sunlit and shaded SLA is calculated, allowing the distribution of sunlit and shaded leaves to be altered by time of day (see Thornton and Zimmerman, 2007 for further details).

8.1.3 SPA

The canopy structure is SPA is layered (in our model simulation a 3 layered canopy) with a vertical pattern of LAI which was set to 40% in the top layer and 30% in the

second and third. Leaves are distributed in each layer assuming a spherical leaf angle distribution and no leaf clumping. In each layer leaves area split into sunlit and shaded fractions and as with CLM a sunlit leaf defined as a leaf receiving both direct and diffuse radiation and a shaded leaf defined as a leaf only receiving diffuse radiation. The proportion of radiation absorbed by each canopy layer is determined by:

$$P=\exp(-GLi/\mathrm{Sin}B) \qquad \textit{Equation 2}$$

Where P is the proportion of incident light absorbed, G is 0.5 assuming a spherical leaf angle, *L*i is the leaf area of the canopy layer and B is the elevation of the radiation source, which varies with latitude and time of day. Photosynthesis is altered thorough the canopy according to an exponential decay in leaf nitrogen content.

8.1.4 ED

The canopy in ED is the most complex in this study. The canopy in ED represents the canopy of a stochastic gap model described by (Moorcroft et al., 2001). The ED model splits model grid-cells into 'patches' which represent areas of the grid cell that have a similar disturbance history. A series of partial differential equations are then used to approximate the effect of stochastic disturbance effects on the size and age structure of trees of different successional groupings, (C4 grasses, and early, mid and late successional trees). A detailed description of the ED version 2 model can be found in Medvigy et al., 2009).

8.2 Moisture responses on GPP

Below is a description of how changes in moisture availability can affect GPP across the four models.

For the CLM, ED, and SiB models net photosynthesis (A_n) can be altered by changes in atmospheric through the effect of air humidity on leaf stomatal conductance (g_s). A_n responds to changes in soil moisture according to a moisture stress factor (described below) which is used to alter stomatal conductance and A_n directly. Stomata conductance for ED, CLM, ED and SiB is determined using Equation 3 taken from Collatz et al., (1991):

$$gs = \left(m\frac{A_n\, h_s}{c_s} + b\right)\beta \qquad \textit{Equation 3}$$

Where m is the slope (set to 9 in all three models), A_n is the rate of CO_2 uptake, h_s is the relative humidity, c_s is the mole fraction of CO_2, b is the intercept set to the minimum stomatal conductance (2 mmol m^{-2} s^{-1} in CLM and 10 mmol m^{-2} s^{-1} in ED and SiB) and β is a soil water stress factor (a value of 0-1, where one represents no water stress and 0 represents complete restriction by water stress, see section 8.4). Equation 3 is adapted slightly in CLM to use total rather than net photosynthesis (see Oleson et al., 2004 for details).

The SPA model solves for g_s using a complex routine which optimises A_n through allowing the maximum possible g_s without letting the leaf water potential drop below

a critical level (-2.5 MPa). Unlike the other models, SPA models the plant hydraulics in more detail and simulates the resistance to water transport from the soil to the leaf, in relation to the soil and leaf water potential. A detailed description of the hydrology of the SPA model can be found in Williams, (1996).

8.3 Temperature dependencies of GPP

Below is a description of how changes in temperature can affect GPP across the five models.

All of the models derive their photosynthesis schemes from adaptations of the equations from Kirchbaum and Farquhar, (1984) and Farquhar et al. (1980).

8.3.1 CLM & SiB

In CLM, and SiB the equations used are those described in Collatz et al (1991). In these models net photosynthesis (A_n) is derived as the minimum of the rate of the rubisco limited rate of photosynthesis (W_c), the light limited rate of photosynthesis (W_l) and the transport limited rate of photosynthesis (W_e), minus the leaf respiration which is assumed to be 0.015 of V_{cmax} (Collatz et al., 1991). Leaf respiration is determined as a constant fraction of carboxylation by Collatz et al. (1991). Calculation of W_c is dependent on the Michaleis-Menton constants which determine the rate of carboxylation and oxygenation reactions (K_c and K_o). K_c and K_o are dependent on temperature (T) as follows:

$$K_c = K_{c25} \cdot 2.1^{(T-298.15)/10}$$ *Equation 4*

$$K_o = K_{o25} \cdot 1.2^{(T-298.15)/10}$$ *Equation 5*

K_{c25} and K_{o25} are the rates at 25°C which are set to 30 PA and 30000 PA respectively, in both CLM and SiB. The values of 2.1 and 1.2 represent the rate on increase with a 10°C rise in temperature (Q10).

The maximum rate of RuBP carboxylation (V_{cmax}) is used in the calculation of W_c and W_e. V_{cmax} is calculated using the following equation:

$$V_{cmax(T)} = (V_{cmax25} \cdot Q10^{\frac{(T-298.15)}{10}}) \cdot f(t) \cdot \beta$$ *Equation 6*

Where V_{cmax25} is set to 60 µmol m^{-2} s^{-1} in CLM and 100 µmol m^{-2} s^{-1} in SiB, and where the Q10 (the rate of increase in activity for a 10°C increase in temperature) is 2.4 in CLM and 2.1 in SiB. F(t) is a temperature response function which causes the V_{cmax} to decline after an optimum point which is between 35-36°C in both models (see Figure 5.2). Both models apply the β to V_{cmax} as a mechanism of down-regulating A_n in water stress conditions. CLM and SiB both integrate their V_{cmax} though the canopy according to leaf nitrogen which is varied with canopy position. The light limited rate of photosynthesis does not have a temperature response in

these two models; it is a function of a quantum yield parameter and incoming radiation (see Collatz et al., 1991).

The CO_2 compensation point ($\Gamma*$) for photosynthesis is used in the calculation of W_c and W_j. The temperature response on $\Gamma*$ in CLM is determined according to Equation 7 taken from Oleson et al. (2004):

$$\Gamma_* = 0.5\left(\frac{2.4}{0.69}\right)0.21P_{atam} \qquad \textit{Equation 7}$$

Where 2.4 is the Q10, 0.69 is the nitrogen limitation factor and $0.21P_{atm}$ is the O_2 concentration at atmospheric pressure (Pa).

In SiB $\Gamma*_{is}$ determined according to the Equation 8 taken from Table 2 in Sellars et al., (1992):

$$\Gamma_* = 20900/2(2600 \cdot 0.57^{\frac{(T-298.15)}{10}}) \qquad \textit{Equation 8}$$

Where 20900 represents the O_2 concentration (Pa) at atmospheric pressure, which is divided by 2 multiplied by a CO_2 / O_2 specificity function.

8.3.2 SPA

In SPA A_n (Equation 9) is determined using the minimum of the limit on photosynthesis by rubisco (W_c) and the limit by RuBP regeneration (W_j), combined with Γ_*, the CO_2 concentration inside the leaf (C_i) and leaf respiration (R_d).

$$A_n = \min(W_c, W_j)(1 - \Gamma_*/C_i)R_d \qquad \textit{Equation 9}$$

W_j is determined by a light limitation and the electron transport limited rate, which is modelled using J_{max}, unlike SiB and CLM which assume the transport limited rate is half of V_{cmax}.

The temperature response functions in SPA are derived from the McMurtrie et al. (1992). In this version of the Farquhar equations both V_{cmax} and J_{max}, which are used to calculate W_c and W_j have a temperature response determined by:

$$V_{cmax} = N\ \tau_{tc}\ k_c \qquad \textit{Equation 10}$$

$$J_{max} = N\ \tau_{tj}\ k_j \qquad \textit{Equation 11}$$

Where N is the leaf nitrogen content, τ_{tc} and τ_{tj} are the temperature coefficient and k_c and k_j are the catalytic rate coefficients set to 15 and 30 μmol m^{-2} s^{-1}. τ_{tc} and τ_{tj} are determined using temperature response curves described in Rastetter et al. (1991) fitted to a polynomial relationship described in McMurtrie et al. (1992). The

temperature optimum for the polynomial relationship is set to 30 °C.

The temperature dependencies for K_c, K_o and Γ_*, which are used to calculate W_c and W_j are taken from McMurtrie et al. (1992) and determined by:

$$K_c = 310\ e^{23.956(T-298.15/T)} \qquad \textit{Equation 12}$$

$$K_o = 155\ e^{14.509(T-298.15/T)} \qquad \textit{Equation 13}$$

$$\Gamma_* = 42\ e^{9.46(T-298.15/T)} \qquad \textit{Equation 14}$$

The rate of carboxylation (V_c) is then determined using the minimum of either the rubisco carboxylation rate which is derived from V_{cmax} or the RuBP regeneration rate which is derived from J_{max}.

The calculation of leaf respiration includes an exponential temperature response with a Q10 of 2:

$$R_d = 0.05 n_l\ e^{\log(2)(T-283.15/10)} \qquad \textit{Equation 15}$$

8.3.3 ED

ED calculates A_n according to Equation 16 taken from Medvigy et al. (2009):

$$A_n = (\min(W_e, W_c) - R_d)\beta \qquad \textit{Equation 16}$$

Note that in ED the soil water stress factor is applied directly to A_n, not V_{cmax} as in CLM and SiB.

V_{cmax} is used to calculate W_c and is calculated according to Equation 17, taken from Medvigy et al. (2009).

$$V_{m(T)} = V_{mo} \frac{\exp(3000(\frac{1}{288.15} - \frac{1}{T})}{(1+\exp(0.4(T_{lo}-T))(1+\exp(0.4(T-T_{hi}))} \qquad \textit{Equation 17}$$

Where V_{mo} is V_{cmax} at 15°C, set to 18.75, 12.5 and 6.25 μmol m^{-2} s^{-1} for early, mid and late successional trees, respectively. The equation is an exponential response but it has two temperature cut-off points T_{lo} and T_{hi} which are set to 8°C and 45°C respectively. The Michaelis–Menton constants used for calculating W_c are calculated using the same format as CLM and SiB (Equations 3 and 4). Γ_* is calculated in according using equation 17 taken from Medvigy et al 2009:

$$\Gamma_* = (21.2\text{ppmv})\exp(5000\left(\frac{1}{288.15} - \frac{1}{\mathrm{T}}\right)) \qquad \textit{Equation 18}$$

As in SiB and CLM R_d in ED is determined as 0.015 of V_{cmax}.

8.4 Calculation of the β factor

In CLM, ED and SiB β is a value decrease from 1 to 0 within increasing soil water stress and is used to down-regulate stomatal conductance and photosynthesis, either directly (ED) or through down regulating V_{cmax} (CLM and SiB). β replaces the effect of the detailed connection of stomtal conductance to leaf and soil water potential in SPA. β is directly calculated from plant available soil water and root density, but is calculted slightly differently between models.

8.4.1 CLM

$$\beta = \sum_i \beta_i B_{ri} \qquad \textit{Equation 19}$$

$$\beta_i = \left(\frac{\psi_i - \psi_w}{\psi_{so} - \psi_w}\right) \qquad \textit{Equation 20}$$

Where β_i is the soil water stress factor for each soil layer (i), B_{ri} is the fraction of root biomass in a soil layer, ψ_i is the soil water matrix potential in soil layer i, ψ_{so} is the soil water matrix potential when stomata are fully open and ψ_w is the soil water potential at wilting point.

8.4.2 ED

$$\beta = \sum_i \frac{1}{1+\frac{D}{S_i}} \qquad \textit{Equation 21}$$

$$D = ET_m\ LAI$$ *Equation 22*

$$S_i = K_w\ \theta_i\ B_{ri}$$ *Equation 23*

Where ET_{m} is maximum evapo-transpiration, LAI is leaf area index, K_{w} is a soil-plant conductivity parameter, and θ_i is the volumetric soil water content per soil layer.

8.4.3 SiB

$$\beta = \sum_i \left(\frac{1-\frac{\theta_{wp}}{\theta_i}}{1-\frac{\theta_{wp}}{\theta_{fc}}} \right) B_{ri}$$ *Equation 24*

Where θ_{wp} is the volumetric soil water content at wilting point and θ_f is the volumetric soil water content at field capacity.

8.5 References.

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Chapter 9: (Appendix 3) Co-author publications

In this section I list other manuscripts on which I am a co-author as a result of the research completed during my PhD.

9.1 Ecosystem respiration and net primary productivity after 8 - 10 years of experimental through-fall reduction in an eastern Amazon forest.

Antonio C. L. da Costa, Daniel B. Metcalfe, Chris E. Doughty, Alexandre A. R. de Oliveira, G. F. C. Neto, Mauricio C. da Costa, Joao de Athaydes Silva Junior, Luiz E. O. C. Aragão, Samuel Almeida, David R. Galbraith, Lucy M. Rowland, Patrick Meir, Yadvinder Malhi

Accepted in Plant Ecology and Diversity, 2012

*I contribution the analysis of the litter-fall data to this paper

9.2 How does nutrient availability influence rates of leaf respiration across Tropical Rainforest?

Zaragoza-Castells, J., Meir P., Atkin O., Lloyd J., Bloomfield K., Rowland L., Salinas N., D., B., M, T.

Paper in preparation, to be submitted in 2013

*I contributed to the research design, data collection, and data analysis of this paper

9.3 Evaluating model predictions of carbon fluxes for Amazonian rainforests subjected to severe drought.

Powell, T.L., Galbraith, D., Christoffersen, B.J., Harper, A., Imbuzeiro, H.M.A., Rowland, L., M., B.P., Da Costa, A.L., Costa, M.H., Levine, N.M., Malhi, Y., Saleska, S.R., Williams, M., Meir, P., Moorcroft, P.

Per in preperation, to be sublitted in 2013

*I contributed model simulations to with the SPA model to this paper and contributed to the research structure.

9.4 Plant water availability in ecosystem models applied to Amazonia: The role of root uptake under normal and simulated drought conditions.

Christoffersen, B.J., Imbuzeiro, H.M.A., Powell, T.L., Galbraith, D., Harper, A., Rowland, L., M., B.P., Da Costa, A.L., Costa, M.H., Levine, N.M., Malhi, Y., Williams, M., Meir, P., Moorcroft, P., Saleska, S.R.

Paper in preperation, to be submitted in 2013

*I contributed model simulations with the SPA model to this paper and contributed to the research structure.